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THE MODE OF TRANSMISSION OF NON-CYST-FORMING FLAGELLATES IN THE OVOVIVIPAROUS YUCCA NIGHT LIZARD *XANTUSIA VIGILIS*

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Ever since Wood (1935) commented on the presence of non-cyst-forming microorganisms in the intestines of desert-inhabiting lizards, there has been speculation as to how transmission of such apparently delicate protozoans is effected in a desert climate. Since the desert lizards of Southern California are, for the most part, insectivorous, suggestions have been made for possible arthropod transmission, incriminating coprophagous insects feeding on lizard feces as vectors, the arthropods in turn being ingested by the saurians. No experiments or critical investigations were made, however, and the proposed insect transmission remained a mere hypothesis.

During an intensive study of the intestinal entozoa of the California night lizards in the past two years, it has been possible to shed some light on the exact mode of transmission of these non-cyst-forming intestinal flagellates. Experiments were carried out particularly with *Xantusia vigilis,* the yucca night lizard from Antelope Valley in the Mojave Desert, since this species of lizard appeared to harbor more non-cyst-forming flagellates than any other sympatric desert form.

METHODS

Investigations of the intestinal fauna in *X. vigilis* had shown that among ten kinds of entozoa, ranging from flagellates through helminths, there were commonly encountered at least three intestinal flagellates which have never been known to form cysts: *Monocercomonoides lacertae, Monocercomonas colubrorum,* and *Tritrichomonas augusta.* These three intestinal entozoa appear to be harmless commensals of their saurian hosts.

Practically all of the 400-odd *X. vigilis* examined showed a natural infection with at least one kind of these flagellates. In order to study transmission it was therefore necessary somehow to obtain lizards known to be free from natural infection with such flagellates.

Medication of the lizards with such drugs as atabrine, carbarsone, and aureomycin, either administered orally or as "high enemata," proved ineffective in clearing flagellate infection completely. Exposure of the lizards for prolonged periods of time to sublethal high (38° C), or cold (2° C), temperatures also had no effect in ridding the lacertid hosts of their intestinal flagellates. Finally two methods were found to be effective in producing flagellate-free *X. vigilis.*

1. *Aseptic surgical delivery of young lizards.* By aseptic Caesarian delivery,

[1] This material was included in a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, University of California, Los Angeles. The author wishes to express his gratitude to Professor Gordon H. Ball under whose guidance this work was done.

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young yucca night lizards near term could be obtained in early September and then raised in isolated and uncontaminated cages in the laboratory, thus providing "clean" animals for experimental purposes. As the exact timing for surgical intervention, yielding young lizards capable of surviving such premature birth is rather difficult, and since the animals are at best of small size, this method, although practicable, was later abandoned in favor of the second one.

2. *Defaunation by oxygenation.* Modification of the classical work by Cleveland (1925) for defaunating termites by exposure to pure oxygen made it possible to obtain flagellate-free *X. vigilis* of any age by exposure of the lizards to pure oxygen at 2 atmospheres (4° C) for 7 days. A specially designed pressure tank made this procedure an easy one once the proper pressures, temperatures, and timing had been worked out (Fig. 1).

For the transmission studies, properly marked flagellate-free *X. vigilis* were placed in large terraria with desert sand together with freshly collected yucca night lizards and left for two months. Other flagellate-free lizards were placed in containers with presumably contaminated sand from a large stock cage of lizards and also left for two months. Controls consisted of oxygenated and Caesarian-delivered *X. vigilis* kept in cages with sterilized sand. All lizards were fed on larval *Tenebrio molitor.* These larval mealworms could never be made to pick up any infection with lizard flagellates even when fed practically pure cultures of these protozoans. Furthermore, a study of the normal intestinal fauna of a large number of larval and adult *Tenebrio* from stock cultures never revealed any intestinal flagellates of the kind found so commonly in *X. vigilis.* It appears thus that the only way in which mealworms could possibly aid in transmission of saurian flagellates is in a purely mechanical way, *i.e.,* by contamination, but never in the nature of a host.

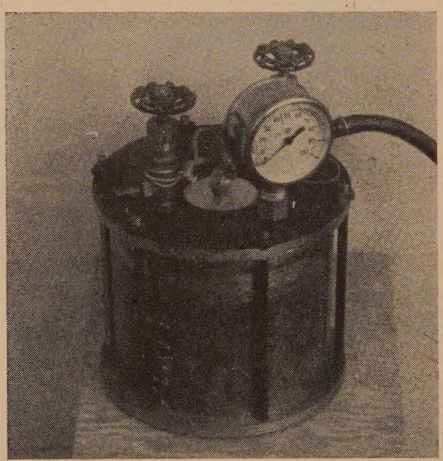

FIG. 1. Pressure tank used for oxygenation of *Xantusia vigilis.*

RESULTS

Examination of the experimental xantusiids showed that while the controls remained free from flagellate infection, although fed the same food as the experimental animals, the "clean" lizards placed in cages with naturally-infected *Xantusia,* collectively exhibited infection with all of the non-cyst-forming intestinal flagellates that had been demonstrated for *X. vigilis* in this investigation. Even among those clean *Xantusia* left in cages with contaminated sand but without any other lizards, some of the lizards acquired flagellate infections of one kind or another.

The data show that in the complete absence of any arthropods, excepting the mealworms mentioned previously, these experimental *X. vigilis* acquired all the non-cyst-forming flagellates peculiar to the yucca night lizard.

CONCLUSIONS

The fact that infection with non-cyst-forming intestinal flagellates of known "clean" *X. vigilis* could be demonstrated in the laboratory in the absence of any suspected arthropod vectors, proves that insect transmission is not necessary to

FIG. 2. Fallen and decaying Joshua tree logs, typical habitat of *Xantusia vigilis*.

effect the spread of fragile non-cyst-forming flagellates among the desert lizards. The repeatedly negative results when looking for lizard flagellates among desert arthropods seem to rule out further such a mode of transmission.

It appears that direct transmission by contamination plays the major, if not the only, role in the spread of these flagellates from lizard to lizard. The peculiar habitat of the yucca night lizard may well be one of the factors that is responsible for the high infection rate of non-cyst-forming flagellates present in this lizard. Its secluded niche under decaying Joshua tree (*Yucca brevifolia*) logs where there is considerable retention of moisture even in the desert, favors flagellate transmission by contact with contaminated soil (Fig. 2). Furthermore, the nocturnal habit of this species of lizard, restricting its foraging to periods when surface temperatures are at a minimum, also renders direct transmission more successful. Finally, ovoviviparity of these lizards, where there is a good chance for initial infection to occur during the emergence of the fetus through the entozoa-contaminated maternal cloaca, undoubtedly accounts for the persistently demonstrable flagellate infection in the newly born *X. vigilis*. Cowles (1944) first described the now well-known behavior of the parent lizard during parturition; as the fetus emerges from the cloaca, the parent grasps the fetal envelope in her teeth and rips it open. This permits free passage of infection from the parent to the offspring. Since the infection is not acquired prior to birth, and as even in the laboratory the majority of the normally-born lizards show flagellates in their intestines ten to twelve hours following birth, such infection during birth must play a major role in the case of *X. vigilis*.

SUMMARY

1. The mode of transmission of non-cyst-forming intestinal flagellates naturally occurring in the yucca night lizard of the Mojave Desert was studied.

2. Transmission experiments were conducted with Caesarian-delivered flagellate-free and defaunated lizards which were exposed to normally infected *Xantusia vigilis* and to contaminated soil.

3. The findings of this investigation indicated that arthropod transmission for these fragile entozoa is not required and that infection with such non-cyst-forming flagellates may be acquired by direct contamination. The peculiar habitat and behavior of this species of lizard, as well as its ovoviviparity, seem to make possible direct transmission of non-cyst-forming flagellates, even in a desert climate.

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ECOLOGY OF PREHISTORIC ALEUTIAN VILLAGE SITES[1]

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Prehistoric Aleutian village sites are unique in that they possess characteristic vegetational and topographical configurations which set them distinctly apart from other habitats. Their features are easily distinguished from the surrounding landscape even at a great distance. This peculiarity led William Dall (1877), Jochelson (1925: 21–23), and Hrdlička (1937) to suggest the possibility that differences in vegetation might indicate the relative age of such sites.

This idea is, of course, not new to archaeology, nor is the application confined to the Aleutians, for vegetational patterns have been utilized as indicators of previous human activity by an increasing number of workers in recent years, especially in Europe, where there has perhaps been more awareness of human ecology. Worsaar studied succession of vegetational types in Danish peat profiles and discussed the possibilities of viewing prehistoric cultures against a background of evolving floras (Daniel 1950: 303), and an impressive number of Europeans have used surface vegetational patterns as observed from the air during archaeological reconnaissance. Sir C. Fox and O. G. S. Crawford were among those to develop the technique in England where it has been widely used. In America a few archaeological surveys have included an inventory and interpretation of plant cover, *e.g.*, H. M. Zeiner has shown that vegetation on the Angel Mound (Zeiner 1945) could indicate the exact area of primitive occupation quite independently of archaeological excavation. Kroeber (1947: 206) has discussed culture in relation to environment, writing, "Plant cover is obviously almost always likely to stand in relation to culture. It largely expresses climate; it tends heavily to determine the fauna; and it enters directly into subsistence, besides at times affecting travel and transport. It is rather surprising, in fact, that culture is not therefore a function of natural vegetation to a greater degree than actually obtains. That it is not, suggests the preponderant strength of purely cultural forces."

One of the objectives of the writer's Aleutian investigations was to determine the nature and cause of vegetational peculiarities on old village sites and refuse heaps. This particular study was part of a larger program of correlated anthropological and biological field work (Bank *et al.* 1950) sponsored by the University of Michigan.[2] Studies in anthropology were conducted by the writer, Janet F. Bank, and Albert C. Spaulding of the University of Michigan; W. R. Hurt, University of South Dakota; and D. S. McClain, Trinity College, Connecticut. Botanical studies were made by the writer, L. H. Jordal, and H. A. Miller, University of Michigan. During the 1950 and 1951 seasons, T. C. Parks, University of Washington, undertook zoological studies on Adak, and archaeological work in 1951 was efficiently aided by volunteer assistants K. K. Bay, Walter N. Dyakanoff, Jane E. Phillips, and Noel L. Wyatt.

In order to coordinate field studies ashore with observation from the air,

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landings were made on more than 20 islands during eighteen months of 1948–49 and again during the summers of 1950–51. While ashore it was possible to visit a number of prehistoric villages and refuse mounds, some of which were hitherto unreported, and to study their vegetational and cultural characteristics by means of ecological transects across them as well as by archaeological excavation. Definitive reports on the cultural findings will be published later, and hence these data are treated only superficially in this paper.

Aleutian Villages

Every scientific observer in the Aleutians comes away with the realization that practically every island, no matter how small, has contained native villages. Each bay, inlet, cove and bight which affords protection from the worst storms was probably inhabited at one or more times during the period of Aleut occupation of the Aleutian Arc. Many narrow isthmuses along the coasts of even the rockiest islands also show village remains, and small kitchen middens or refuse piles representing temporary fish camps are found almost everywhere. The large number of Aleutian villages drew comment from early Russian explorers, many of whom estimated the population of the Archipelago to surpass 20,000 persons. Such an estimate may have been too high, for early attempts at census taking, when the population had already dwindled, placed the number of surviving Aleuts at only 1,900 (Petrof 1884: 33). Kroeber (1947: 135) gives the figure 16,000 for the estimated population at the time of Bering's visit in 1741. Since that date the Aleuts have almost entirely disappeared through mass slaughter by early Russians, introduced diseases, and starvation. Of the 90 to 150 or more villages which probably existed in 1741, less than a dozen remain (Fig. 1). Instead of 16,000 or more Aleuts then, less than 1,200 are alive today, and half of these reside outside of their original homeland.

Prior to Bering's visit the appropriateness of a location for a village seems to have been a reasonably nearby source of fresh water, which in the Aleutians is nearly always at hand, and a fairly protected stretch of beach for landing the

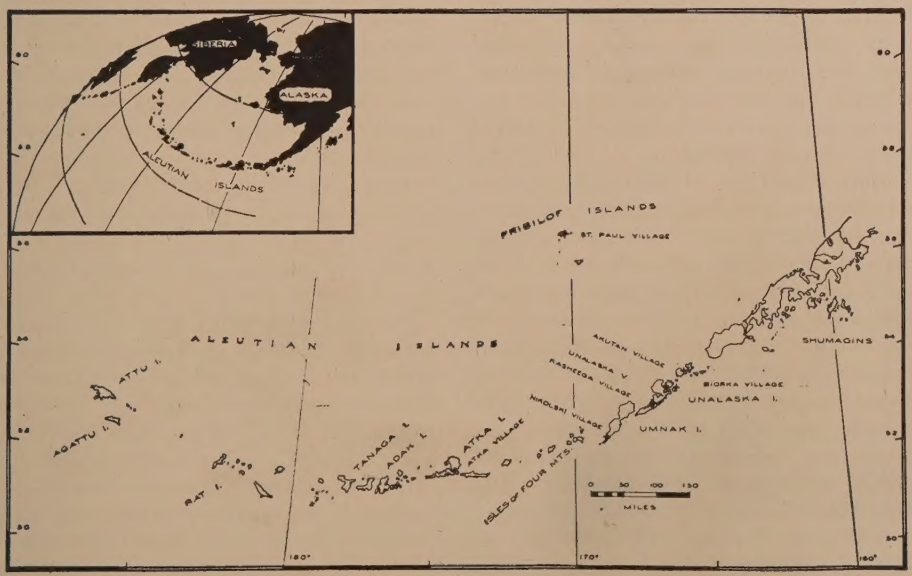

Fig. 1. The Aleutian Arc. Inhabited villages in the Aleutian Islands are shown.

skin boats (bidarkas). However, the latter was actually a minor consideration, for the boats were extremely maneuverable and light. Escape from enemies was especially important to the Aleut. According to Russian accounts (Jochelson 1925: 23 and Petrof 1884: 146–151), Aleut villages during the early years of Russian discovery were mostly located on points of land and narrow isthmuses. Since the Aleuts frequently engaged in inter-island conflict, a good view in two directions and ready access to an escape route by water were of vital importance to them. Attack by a superior force might necessitate hurried transporting of all skin bidarkas across land to provide for the retreat of the entire village; hence many villages were located so that there would be ocean on two sides. The early Aleuts also made use of hills near their villages as lookout posts, in order to avoid surprise by enemies, but also to detect sea mammals which furnished much of their diet. After the Russians brought an end to local warfare, the villages were gradually moved to protected bays and river mouths (Fig. 2). The advantages of better fishing, protection from storms, and more room made the occupation of the more favorable sites highly desirable. Also, the Russians themselves frequently brought together the inhabitants of several villages at a single location for easier administrative control.

Old villages varied from a half acre to ten acres in extent and might consist of five, twenty, or even more than fifty underground dwellings (barabaras). Prior to Russian influence, the Aleuts built these barabaras with an entrance through the sod-covered roofs but later modified them, presumably under direction from the Russians, by placing the doorway in the sides. The earthen walls of the dwellings were frequently reinforced with driftwood, whale bones, and large slabs of stone. Over the driftwood and whale bone rafters, woven grass matting, dried grass and sod were usually laid. One or more families occupied such a dwelling; if more than one, portions of the inside were separated by grass mats. Larger communal barabaras were occasionally constructed, in which many families lived, but the Aleut use of kazims, *i.e.*, large, separate council houses, has not been established.

The remains of Aleut dwellings are seen in section during archaeological excavation. Since abandonment they have caved in, but supporting rafters and soil strata peculiar to them mark their positions in the earth. A sectional view of one such collapsed barabara uncovered on Unalaska is shown (Fig. 3). Immediately below the old floor of the dwelling and to either side are usually found layers of sea urchin shell, fish bone, and intermingled bones of sea mammals, as well as cultural remains. Burials were sometimes made in the earthen walls and sealed up with stone and soil; these are occasionally apparent during archaeological excavation.

Procedure

Selection of sites for study depended largely upon convenience and accessibility, for transportation was available only as military needs provided. A number of village locations were obtained by interrogation of Aleuts; others were incidentally discovered in the course of botanical investigations. Time ashore at any one site was always conditioned by the weather and the necessity of conforming with military schedules.

Our field parties located more than 60 archaeological sites ranging from the Shumagin Islands in the east to Attu in the west. Sixteen of these, located on 10 islands, were given only surface study. Archaeological excavations were completed at sites on 4 of the islands. In order to avoid repetition, several of the more representative sites may serve as examples. Results from these are closely agreeable with others, except that the Nikolski mound (Umnak Island) was noticeably different and is discussed separately. The ancient village sites treated in this paper are Krugloi Point (Agattu), Campers Cove (Adak), Waterfall Site

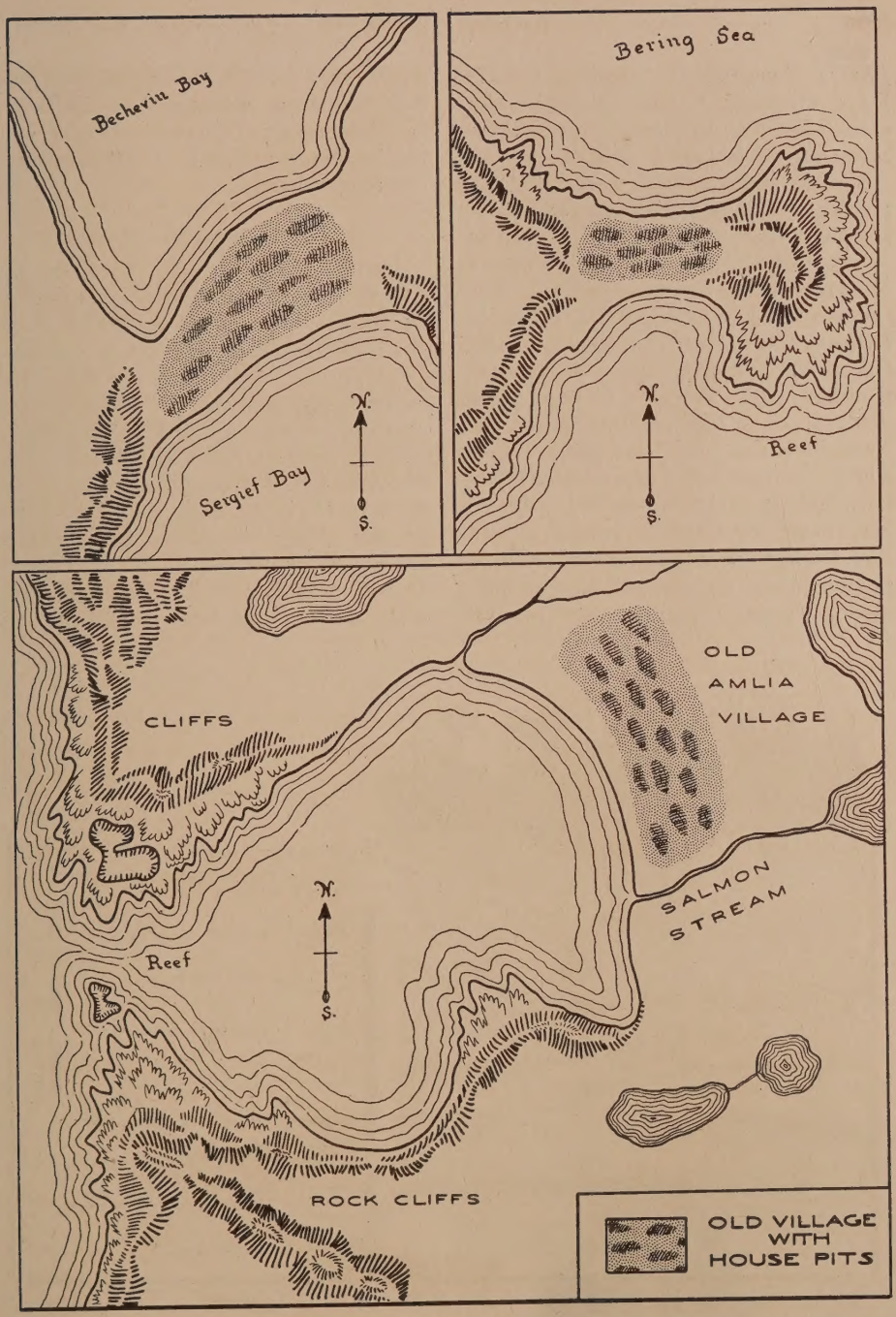

FIG. 2. Pre-Russian and post-Russian village sites in the Aleutians. Upper left: Sergief Bay, Atka Island; upper right: Bluefox Bay, Atka Island. Both are typical pre-Russian sites, which were located on isthmuses and points and offered an easy route of escape in case of hostile attack. Bottom: small cove on western tip of Amlia island, a sheltered village location preferred after 1741.

(Atka), Amaknak-D (Amaknak), Eider Point (Unalaska), and Nikolski (Umnak). The map in Figure 1 gives the locations of the islands.

Detailed measurements were not always feasible because of insufficient time ashore. However, study transects were used whenever possible, and numerical estimates of plants were supplemented by check counts, photographs, and plant collections. Distance was measured by pacing or steel tape. All transects were arbitrarily established with due regard to vegetational patterns and special features on the site. They varied in length but were 10 feet wide. Each extended into adjacent habitats, and, in addition, control strips on non-village areas were examined. Quadrats 10 feet square at various intervals provided data for counts. Several hundred soil samples were collected from different sites and at varying depths, and these are being examined by specialists in microbiology. Tests of soil pH with the La Motte indicator set supplemented other observations.

Plant Ecological Studies

Beginning in the central Aleutians, the islands of Adak and Atka present old villages which were investigated. The Adak site, hitherto unstudied, lies in Campers Cove on the eastern side of the island facing Kagalaska Straits. It comprises an area approximately 200 feet by 150 feet with 35 evident barabara (house) pits. On Atka island, approximately two miles by dory along the coast southeast of the present village on Nazan Bay, another old site of comparable size was examined. Jochelson (1925: 30–45) reported doing some work at this location in 1910, and

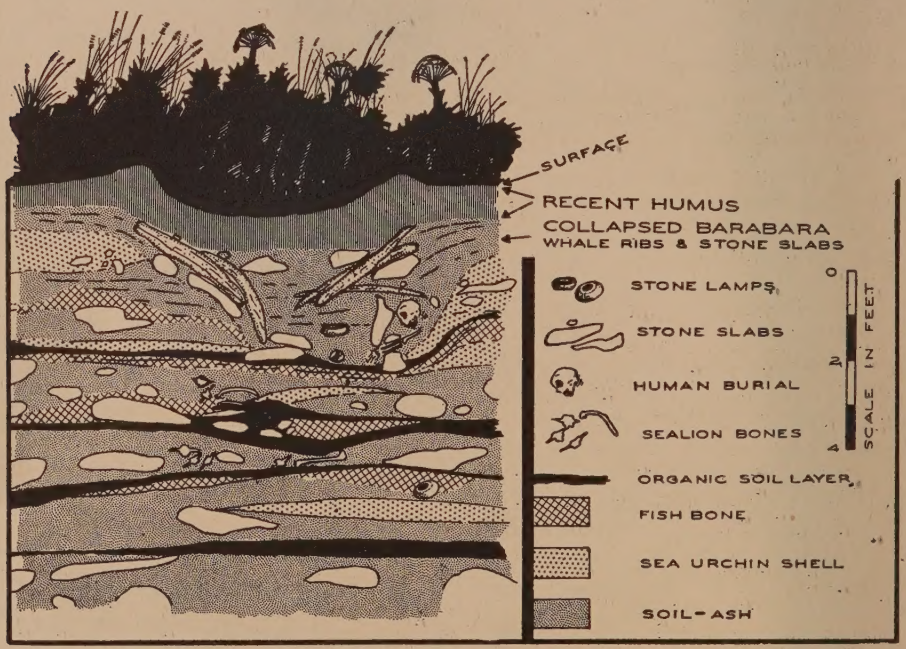

Fig. 3. Diagrammatic profile of an excavation at Eider Point, Unalaska Island. A house pit and subsurface archaeological deposits are shown. Whalebones probably supported the sod roof of the former barabara (underground dwelling of the Aleuts). Roots of surface vegetation, especially *Heracleum*, reached to the shell layers. Typical plants inhabiting former village sites are indicated and include: *Heracleum, Elymus, Angelica, Conioselinum, Achillaea, Claytonia, Ligusticum,* and *Aconitum.*

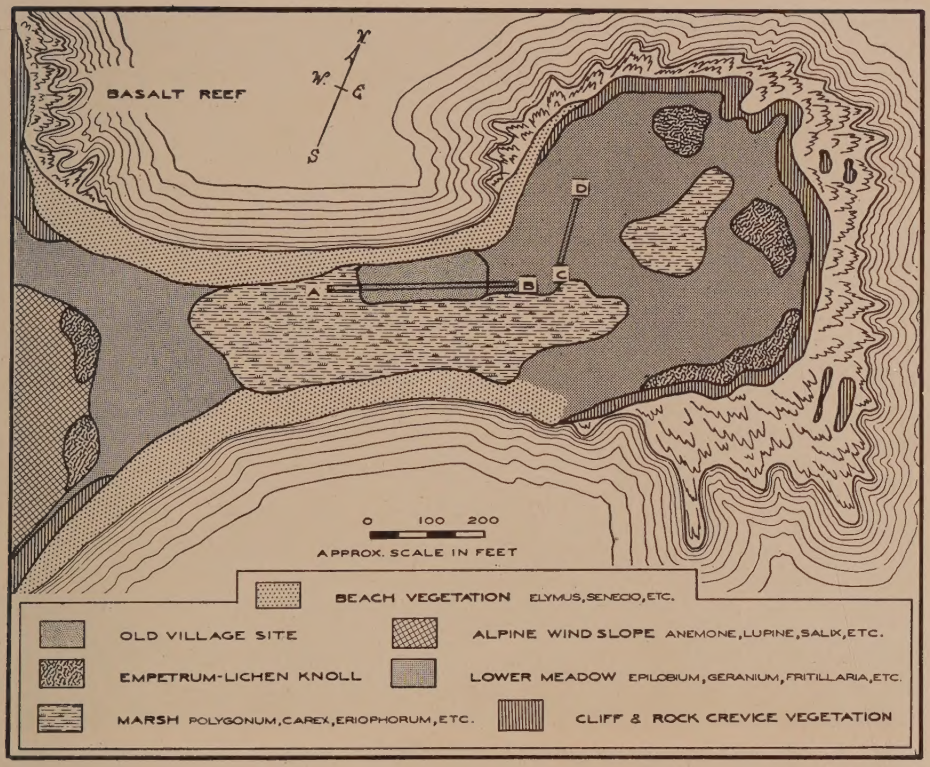

FIG. 4. Old village (waterfall site) and adjacent plant habitats at Nazan Bay, Atka Island. Locations of the study transect (A–B) and the control strip (C–D) are shown. Both are 10 ft. wide. Plants occurring on the transects are given in Table II and in Figure 10.

Hrdlička (1945: 219, 319), referring to it by its present name, the Waterfall Site, excavated here in 1936 and 1937. The writer investigated both sites in 1948 and 1949. At Atka, the study transect extended approximately east and west from a low marshy area, across the old village and thence up a gentle hill on the east (Fig. 4). At Adak, the transect also ran west to east from a lowland meadow, across the site to the beach. A control strip 10 feet wide and 30 feet long was situated entirely within the meadow at a distance of 30 yards from the village boundary. Both villages have been abandoned at least 100 years, according to information received from Aleut informants at Atka. The vegetational composition of these two sites is almost identical to what is found at other old villages at Attu, Tanaga, Amukta and Kagamil and is believed to be representative of all such sites which have not been disturbed recently.

In the eastern Aleutians, two large village mounds are situated at Eider Point on Unalaska Island (Unalaska Bay) and on the southwestern shore of Amaknak Island (Dutch Harbor). It was possible to study both mounds during the course of archaeological excavation. The Eider Point village measures 170 × 280 feet and was found to extend to an excavated depth of almost 30 feet! The point of land lies northwest and southeast. At Amaknak [3] the mound is approximately

[3] Our site is the one Quimby (1946) refers to as midden-D.

FIG. 5. Old village mound at Amaknak Island in Unalaska Bay. A military road constructed in 1942 bisects the mound. Typical old village vegetation can be seen; especially abundant are *Heracleum lanatum* (white umbels), *Elymus arenarius mollis* and *Achillaea borealis*. In some places, especially along the edge of the mound, *Anaphalis margaritacea* var. *occidentalis* and *Epilobium angustifolium* var. *macrophyllum* occur in dense stands. Wartime use of the mound introduced some plants. Three other archaeological sites on Amaknak were destroyed by military construction, and presumably few of the artifacts were saved.

130 × 220 feet, with long axis north and south. Cultural remains were recovered to a depth of 18 feet, below which there are layers of gravel and cobble. Both mounds are largely composed of alternating strata of sea urchin and clam shell, fish bone, and sea mammal bones. Both are said by Aleut residents at Unalaska to be "very old," and neither has been occupied as a village site for at least 150 years. At Amaknak the mound is bisected by a military road constructed during World War II (Figs. 5 and 7). The Eider Point site has likewise been modified by military operations. The uppermost 1 to 3 feet of soil and vegetation were removed in 1942 to clear the area for gun mounts. However, since abandonment of the site by the military in 1945, the vegetation has again grown up and, what is more, there is reproduced what was probably the original plant cover, *i.e.*, species characteristic of all undisturbed old villages studied, with a few introduced additional species, such as *Rumex fenestratus*[4] and *Trifolium repens* which do not normally occur on such sites. The vegetation on the Eider Point mound seems unusually lush, more so than on some other village sites which have not been as recently altered.

[4] Nomenclature in this paper follows that of Hultén (1937 and 1941–1950).

In the western Aleutians, H. A. Miller of our expedition made similar studies at an old village site (Krugloi Point) on Agattu. This village, exposed on a windy point of the extreme northeastern side of the island, is said by the Aleuts to have been abandoned for at least 100 years, probably much longer. Its surface configuration and vegetational pattern are similar to eastern Aleutian villages.

Partial results of these ecological studies are presented for Adak (Table I, Fig. 8), Atka (Table II, Fig. 10), Amaknak (Fig. 7), and Eider Point (Figs. 3, 6). Soil pH figures from 6 inch depths are shown in some cases in addition to indications of plant species occurring on the study strips.

It is evident from these data that soil pH increases as one approaches sites of former human habitation and that the difference in pH between village area and non-village area is substantial. There is also a definite, easily recognized vegetational pattern on villages which is not duplicated on adjacent habitats. It will be shown that this particular plant community is not found anywhere in the Islands except upon abandoned village sites and consists of a mixture of plant species normally associated with three natural habitats, namely: the grass hummock zone near beaches, wet ravines, and the grass meadow habitat of the lowland valleys. I believe that the village vegetation comprises an *association-segregate, i.e.,* an association that has differentiated out of mixed associations of the lowland habitats, in this case not because of climatic influence but as a result of long-persisting edaphic changes brought about

Fig. 6. Diagrammatic profile of a prehistoric mound at Eider Point, Unalaska Island. Distribution of the most abundant plants is indicated by horizontal bars; heavier bars represent greater abundance; broken bars represent scattered occurrence. * *Conioselinum, Ligusticum* and *Angelica* also occur, distributed about the same as *Claytonia.* ** *Achillaea* occurs, distributed much like *Aconitum.* ‡Tall grasses include *Calamagrostis langsdorffii* (*C. canadensis* var. *langsdorffii*), *Deschampsia beringensis, Festuca rubra, Phleum alpinum* var. *americanum.* The *Artemisia* is *A. unalaschensis.* Soil pH values from a 6 inch depth are given at the bottom. Figure 3 is a profile of a single house pit on this same mound and indicates subsurface deposits.

TABLE I. *Plant species and pH values from 10 × 10 ft. quadrats of a transect across an old village site at Campers Cove, Adak Island, Aleutians*

Location of quadrats	Habitat type	Soil pH at 6 inch depth	Plant species most abundant
50 yards west of site	Moist, grassy meadow with gentle easterly slope	5.5	*Agrostis exarata, Festuca rubra, Trisetum spicatum*, etc. *Athyrium filix-femina, Dryopteris* sp. *Platanthera dilatata, Orchis aristata* *Epilobium angustifolium* var. *macrophyllum* *Cornus suecica, Lupinus nootkatensis* (clumps) *Anemone narcissiflora* var. *villosissima*
20 yards west of site	Lush meadow with gentle easterly slope; well-drained	6.0	*Lupinus nootkatensis* (scattered clumps) *Calamagrostis langsdorffii, Festuca rubra* *Deschampsia beringensis*, other grasses *Athyrium filix-femina, Dryopteris* sp. *Anemone narcissiflora* var. *villosissima* *Geranium erianthum, Pedicularis chamissonis* *Cornus suecica, Arnica unalaschcensis* *Fritillaria camschatcensis, Orchis aristata*
Western edge of site	Gentle westerly slope; well-drained	6.0	*Heracleum lanatum, Elymus arenarius mollis* *Calamagrostis langsdorffii, Deschampsia beringensis* *Fritillaria camschatcensis, Geranium erianthum* *Athyrium filix-femina, Aconitum maximum*
Center of site	Hilly and fairly well-drained	7.5	*Elymus arenarius mollis, Heracleum lanatum* *Athyrium filix-femina* (abundant) *Aconitum maximum, Achillaea borealis* *Conioselinum gmelini, Angelica lucida* *Ligusticum hultenii, Claytonia sibirica*
Eastern edge of site	Sloping toward beach on east; wet	7.5	All plants that are found at the center of the site; in addition: *Ranunculus occidentalis* var. *insularis* *Calamagrostis, Deschampsia, Festuca* *Phleum alpinum* var. *americanum*
20 yards east of site bordering on cobble beach	Gentle easterly slope to beach; boulders and driftwood present	6.5	Tall grasses (as above); *Elymus* especially abundant *Senecio pseudo-arnica, Claytonia sibirica* *Honckenya peploides, Cerastium caespitosum* *Mertensia maritima, Lathyrus maritimus* *Cochlearia officinalis, Potentilla villosa*

by man's occupation. The reasons for this view will be presented shortly.

The characteristic plants of this association-segregate are tall members of the Umbelliferae (*Heracleum lanatum, Conioselinum gmelini, Angelica lucida,* and *Ligusticum hultenii*) together with the grass *Elymus arenarius mollis,* and *Claytonia sibirica, Achillaea borealis,* and *Aconitum maximum,* the poisonous monkshood (Fig. 8). *Aconitum* is found in greater abundance on sites in the western Aleutians. Companion plants, *i.e.,* those without any pronounced affinity for this association over another, include ferns (usually *Athyrium filix-femina* but sometimes *Dryopteris* sp.), tall grasses such as *Calamagrostis langsdorffii, Festuca rubra, Deschampsia beringensis,* etc., and occasionally in the east, *Anaphalis margaritacea* var. *occidentalis.* On Kodiak Island, much the same vegetation occurs on old village areas, with the addition of stinging nettle (*Urtica*) and, frequently, elderberry (*Sambucus*). Abundance of characteristic and companion plants are roughly expressed as follows: constantly present (80–100%), *Heracleum, Elymus, Conioselinum, Achillaea,* and in the west, *Aconitum;* mostly present (60–80%), *Claytonia, Angelica, Ligusticum, Calamagrostis, Deschampsia,* and in the east, *Aconitum;* often present (40–60%), ferns and in the east *Anaphalis;* seldom present

(20–40%), *Epilobium, Ranunculus, Cornus,* and *Trientalis;* rarely present (1–20%) are recently introduced plants such as clover and invaders from wet, boggy habitats.

One of the village areas, the Nikolski mound, has a vegetataion which has been greatly modified by man and animals, in this case, sheep. The mound is an imposing structure about 25 feet high, situated just south of the present village of Nikolski on the western end of Umnak Island (Fig. 9). The village is inhabited by 56 Aleuts, the school teacher and her husband. Two of the native houses are situated atop the prehistoric mound. About a half-mile farther south is the white-owned sheep ranch, from which the stock frequently roam over the surrounding territory.

A study strip was established which extended from a stream on the north, over the mound to a shallow lake on the south. The transect was thus about 400 feet long. Vegetation occurring along this strip included: at the stream margin, *Epilobium anagallidifolium, Polygonum viviparum, Juncus balticus, Carex* spp., *Rumex acetosella, R. fenestratus, Caltha palustris, Mimulus guttatus,* and *Equisetum arvense;* north edge of mound where the ground rises sharply, *Ranunculus occidentalis*

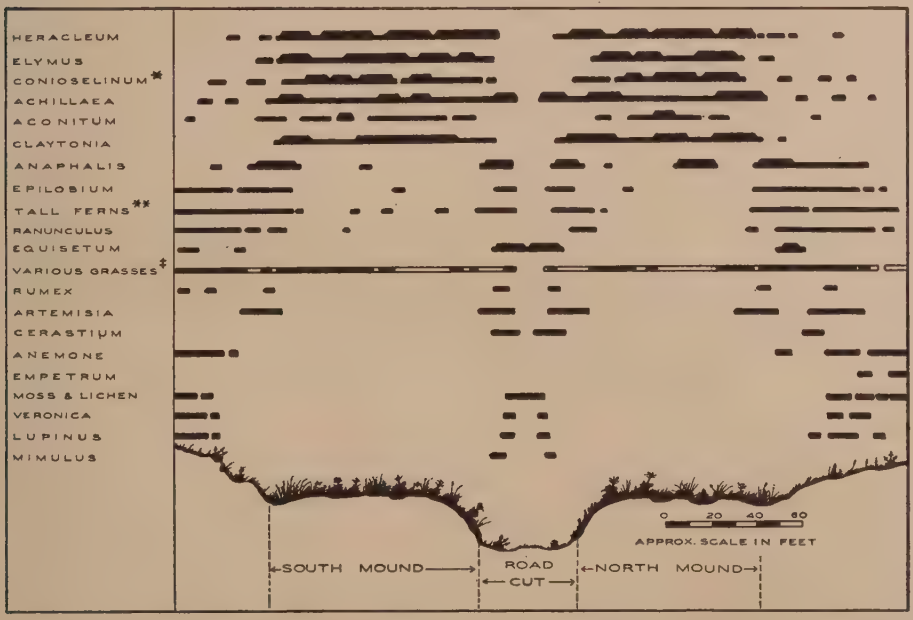

FIG. 7. Diagrammatic profile of prehistoric mound at Amaknak Island, same as shown in Figure 5. Distribution of the most abundant plants is indicated by horizontal bars; heavier bars indicate greater abundance; broken bars represent scattered occurrence. * *Ligusticum hultenii* and *Angelica lucida* also occur predominately on the mound with about the same pattern as shown for *Conioselinum.* ** Tall ferns are *Athyrium Filix-femina,* although some *Dryopteris* also occurs. ‡ Various grasses include those given in the legend below Figure 6, but they are not as abundant here. Other plant species occurring on the transect are: *Heracleum lanatum, Elymus arenarius mollis, Conioselinum gmelini, Achillaea borealis, Aconitum maximum, Claytonia sibirica, Anaphalis margaritacea* var. *occidentalis, Epilobium angustifolium,* var. *macrophyllum, E. latifolium, E. anagallidifolium, Ranunculus occidentalis* var. *nelsonii, Equisetum arvense, Rumex fenestratus, R. acetosella, Artemisia unalaschensis, Cerastium caespitosum, Anemone narcissiflora* var. *villosissima, Empetrum nigrum, Veronica* spp. (unidentified), *Lupinus nootkatensis,* and *Mimulus guttatus.*

var. *nelsonii, Mimulus, Galium aparine, Epilobium angustifolium* var. *macrophyllum, Equisetum,* and sparse short grasses; atop the mound, *Trifolium repens,* short grasses such as *Poa arctica williamsii, Mimulus, Achillaea borealis, Elymus arenarius mollis,* and scattered plants or clumps of *Aconitum maximum* and *Claytonia sibirica;* south of mound near shallow lake, *Trifolium repens, Mimulus, Sphagnum* spp., *Caltha, Rumex acetosella,* and short grasses with some sedges and reeds.

At least two plants have been introduced, *e.g., Trifolium* and probably *Galium,* and the sheep, as well as the constant trampling of the mound by human beings, have greatly influenced both the amount and the kind of plant cover. *Mimulus, Sphagnum* and numerous mosses have invaded, but some of the characteristic old village vegetation is still present, although scattered, *e.g., Achillaea, Claytonia, Elymus,* and *Aconitum.*

At Adak and Atka, individual house pits were stripped of their surface vegetation so that a close census could be made of the plants occurring within them. The figures, together with data from quadrats, gave results which indicated relative abundance of certain plants showing special sensitivity to topographic features on the site. Data for *Elymus, Heracleum, Aconitum, Polygonum,* and *Conioselinum* are graphically presented (Fig. 10). Each dot represents a plant within a strip ten feet wide. Barabara pits are discernible from patterns made by plant species favoring them.

Whereas *Aconitum* seems to show no particuar preference for house pits over any other portion of the village, *Heracleum* is definitely more abundant within the pits. However, at Atka several barabara

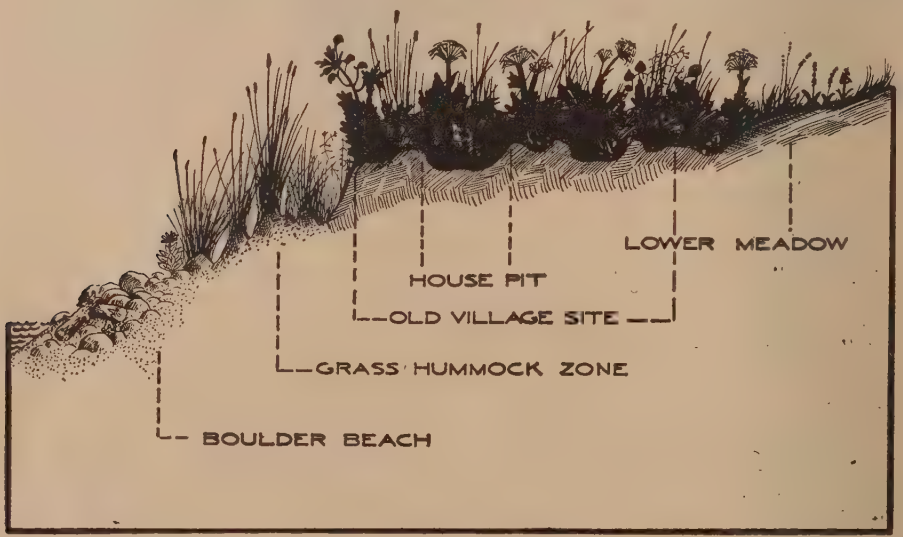

FIG. 8. Diagramatic section of a typical small village site, based on an actual site on Adak, showing barabara pits, lush vegetation usually occurring on old villages, and the characteristically narrow ecotones between the village plant community and adjacent communities. The most abundant plants on the village area are the same as those listed below Figure 3. Occurring in the meadow complex are: *Polygonum viviparum* var. *macounii, Agrostis exarata, Trisetum spicatum, Poa macrocalyx, Festuca rubra aucta, Pedicularis chamissonis, Arnica unalaschcensis, Geranium erianthum, Ranunculus occidentalis* var. *insularis, Barbaraea orthoceras, Epilobium behringianum* and others. Making up the beach and hummock complexes are: *Senecio pseudo-arnica, Lathyrus maritimus, Elymus arenarius mollis* (also *Deschampsia, Calamagrostis,* etc.), *Claytonia sibirica, Mertensia maritima* and others.

TABLE II. *Plant species and pH values from 10 × 10 ft. quadrats of a transect across an old village site at Nazan Bay, Atka Island, Aleutians*

Location of quadrats	Habitat type	Soil pH at 6 inch depth	Plant species most abundant
30 yards west of site	Low, wet marshy area	4.5	*Carex macrochaeta, C. hindsii, C. anthoxanthea* *Eriophorum chamissonis, Juncus balticus* *Polygonum viviparum, Plantago macrocarpa* *Hippuris vulgaris, Rumex acetosella, Equisetum arvense* *Scirpus caespitosus, Luzula parviflora, Poa komarowii* var. *vivipara* *Iris setosa* (1 specimen), *Conioselinum gmelini* (1 specimen)
Western edge of site	Sharply rising ground; wet from seepage of water from site	5.5	*Elymus arenarius mollis, Deschampsia beringensis, Poa* sp. *Heracleum lanatum, Claytonia sibirica, Achillaea borealis* *Conioselinum gmelini, Ligusticum hultenii, Streptopus amplexifolius* *Athyrium filix-femina, Dryopteris* sp. *Cerastium caespitosum, C. fischerianum, Aconitum maximum* *Ranunculus occidentalis* var. *insularis*
Center of site	Moist; uneven surface due to old house pits; about 6 ft. higher than marsh to west	7.5	*Heracleum lanatum, Elymus arenarius mollis, Conioselinum gmelini* *Angelica lucida, Claytonia sibirica, Athyrium filix-femina* *Ligusticum hultenii, Achillaea borealis, Aconitum maximum* *Deschampsia beringensis, Calamagrostis langsdorffii, Festuca rubra* (these grasses scattered over the site) *Ranunculus occidentalis* var. *insularis* (scattered)
Eastern edge of site	Rising abruptly toward east; well-drained	7.0	All plants that are found at the center of the site; *Elymus* is especially abundant *Epilobium angustifolium* var. *macrophyllum* *Fritillaria camschatcensis, Lycopodium clavatum* (scattered)
30 yards east of site	Fairly steep southerly slope; well-drained	5.0	*Poa macrocalyx* (?), *Carex macrochaeta, Trisetum spicatum* *Polygonum viviparum, Pedicularis chamissonis, Arnica unalaschcensis* *Erigeron peregrinus, Cornus suecica, Lycopodium* spp.
50 yards east of site	Dry knoll, very well-drained at all times	4.5	*Lycopodium clavatum* and others, *Cladonia* spp., *Empetrum nigrum* *Cornus suecica, Trientalis europaea arctica, Linnaea borealis* *Veronica stelleri, Phyllodoce aleutica, Poa* spp. (scattered)

pits falling outside of the transect did not show this pattern. These are probably the pits which were excavated in 1936 and 1937 by Hrdlička, and perhaps this would account for the difference. It is tentatively suggested that *Heracleum* grows better within the house pits because of more favorable pH conditions there. Moisture accumulation, *i.e.*, constantly damp soil but no standing water within the pits, is greater than elsewhere on the site, which also may account for the denser growth of cow parsnip in them.

Elymus seems to grow more densely along the periphery of the old village and, too, along the slightly raised margins of the house pits. Perhaps slightly more acid conditions resulting from leaching of the soil accounts for this. Tests as conducted by our group, however, were not sufficiently sensitive to measure minor differences in pH. Although the plotted data indicate dense growths of *Elymus* bordering the house pits they do not show equally dense stands which occur elsewhere on the site. These latter stands, however, are on slightly raised hummocks of about the same height as the pit margins. Quick drainage may be a determining factor of the habitat.

Polygonum viviparum was plotted to show the distribution of a typical plant

occurring frequently in habitats adjacent to the old village. Intolerance to the old village site is marked. However, this is not true of some other widely occurring plants such as the grasses *Deschampsia* and *Calamagrostis,* as well as *Cornus suecica, Ranunculus* spp., *Trientalis europaea arctica,* and some species of *Epilobium,* which seem to grow equally well, although in scattered condition, both on and off old village areas on some of the islands. At Nikolski, this is also true of the introduced clovers (*Trifolium repens*) and *Rumex acetosella.*

On the whole, the midden soils are loosely packed and very porous, due to the archaeological remains, shells, and so forth, contained in them and also because of the high percentage of pumiceous, volcanic ash generally found in Aleutian soils. The soil underlying house pits is less porous than elsewhere on the sites and drainage is poorer. Porosity of the soils is, of course, an important factor regulating the amount of certain chemicals available to plants from the soil. On the other hand, soil saturation with water is high in the Aleutians due to almost constant precipitation, and this, combined with fairly low soil temperatures, causes a low rate of organic decomposition, which in turn makes possible the slow release of certain chemicals from organic matter, over an unusually long period of time. Although no measurements were made to ascertain it, midden soils undoubtedly contain much calcium and probably considerable phosphorus and nitrate in comparison to other Aleutian soils, due to the abundant subsurface fish bone, shell, and other fertilizing deposits. The amount of leaching, which might quickly remove the nitrate, has not been determined, but it is probable that the percentage of nitrate

FIG. 9. Nikolski village, Umnak Island, from the air. Large prehistoric mound is indicated by arrow. Vegetation in this part of the island has been affected by sheep from the ranch shown in the extreme upper left corner. Depressions in the hillside which can be seen just above and to the left of the mound are probably barabara pits and represent another ancient site. (Official U. S. Navy Photograph.)

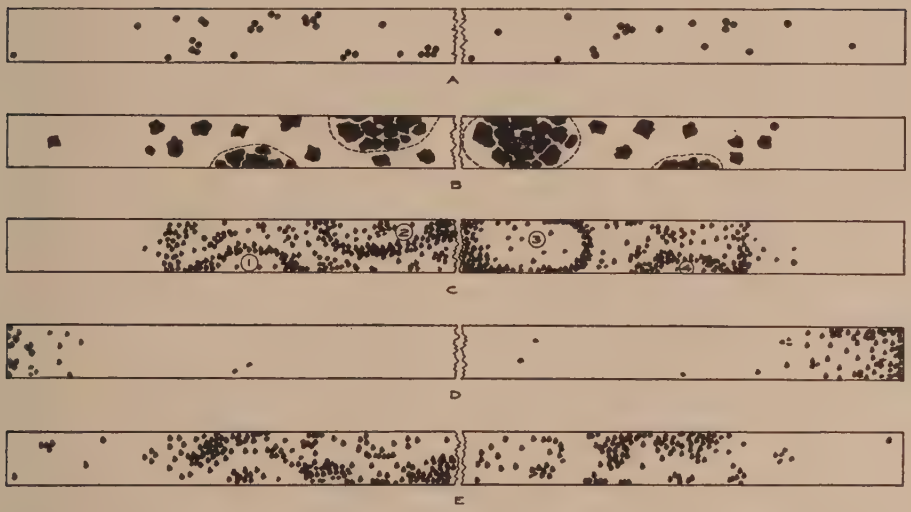

FIG. 10. Diagram showing distribution of certain plant species on the study strip across the former village (waterfall site, Fig. 4, Table II), Nazan Bay, Atka Island. The strip is 10 feet wide and about 330 feet long, but for convenience the middle segment is left out. Plant distribution on this portion of the transect was similar to what is shown within the village boundaries. Each dot represents a plant; thus the diagrams present the distribution of: A) *Aconitum maximum;* B) *Heracleum lanatum,* shows partiality to house pits; C) *Elymus arenarius mollis,* shows partiality to pit margins; D) *Polygonum viviparum,* shows intolerance to village area; E) *Conioselinum gmelini.* Barabara (house) pits, 1–4, are indicated by the patterns of plants favoring them.

in midden soils is greater over a long period of time than it is in non-midden soils in the Aleutians. The availability of the chemicals calcium, phosphorus, and nitrate determines the abundance of certain characteristic plants on old villages, probably more than any other factor. Thus, these, but not all of the plants on old village sites, compose a neutrophilous, possibly a nitrophilous plant community. Among the plants which are most abundant on these sites, *Aconitum,* members of the Umbelliferae, and *Urtica* (on Kodiak) would seem to be fairly reliable indicators of the increased presence of one or all of the chemicals calcium, phosphorus, and nitrate.

In order to complete a description of the vegetational peculiarities of old villages in the Aleutians, it is necessary to consider briefly the typical plant communities of non-village areas and the uses which the former Aleuts made of local plants. The latter subject has special significance in an explanation of village vegetational patterns. Aleutian plant habitats are treated in detail elsewhere and will not be dealth with exhaustively here. The interested reader may wish to refer to Hultén's excellent work (1937) and my own recent paper (1951).

Plant Habitats Adjacent to Old Villages

Except that all villages were located near the sea, adjacent plant habitats vary considerably. The Atka site is bordered by a cobble beach on the north; a grassy meadow slope terminated by an *Empetrum* knoll on the east; a low, wet, grass marsh on the south; and a standing water marsh and seepage slope on the west (Fig. 4). Our site at Campers Cove, Adak, is bordered by a sandy beach, lowland meadow, seasonal mudflat, and lowland stream valley, whereas the Eider Point site is bor-

dered on two sides by a cobble beach and reefs, on the third side by a steep, grassy meadow slope and terrace rock cliffs, and the point of land itself is terminated in a long, jagged basalt reef.

Aleutian beaches have been found to be primarily cobble and boulder, deeply wave-cut, with extensive off-shore reefs and occasional patches, especially in the bays and inlets, of grey to black sand. *Potentilla, Poa,* and lichens inhabit the earth deposits in the crevices of shore rocks, and the cobble and sand beaches possess scattered growths of scurvy weed (*Cochlearia officinalis*), ragwort (*Senecio pseudo-arnica*), beach pea (*Lathyrus maritimus*), and a number of grasses. Slightly back from the beach and occupying the marginal ridges and irregularly surfaced hummock zone will be found an association of wild-rye (*Elymus arenarius mollis*), spring beauty (*Claytonia sibirica*), *Senecio,* and numerous grasses, especially *Calamagrostis langsdorffii, Deschampsia beringensis, Phleum alpinum* var. *americanum,* and *Festuca rubra.* Beyond the hummocks, there usually exist several terraces or rock walls or sometimes steep, grass meadow slopes whose vegetation includes, in addition to *Calamagrostis* and other grasses, geranium (*Geranium erianthum*), lousewort (*Pedicularis chamissonis*), *Epilobium* spp., and numerous smaller plants, *e.g., Trientalis europaea arctica, Geum calthifolium,* etc. Here also occur scattered plants of *Heracleum, Conioselinum, Aconitum,* and *Anaphalis.* Dry knols with thick carpets of tundra berry (*Empetrum nigrum*), lichens (*Cladonia* and others), and mosses, as well as blueberries (*Vaccinium uliginosum* var. *alpinum*) and bunchberry (*Cornus suecica*) usually terminate these hilltops. Stream valleys are frequently choked with lush growths of fern and grasses as well as such plants as the showy orchid (*Orchis aristata*), white orchid (*Platanthera hyperborea*), other platantheras, cucumber plant (*Streptopus amplexifolius*), yarrow (*Achillaea borealis*), and not infrequently *Anaphalis, Epilobium, Artemisia, Angelica,* and *Ligusticum,* with some *Heracleum.* Still higher, where the winds continually blow and greatly restrict plant growth, there occur thin carpets of *Empetrum,* lichens, Ericaceae and heath companions such as anemone and lupine, as well as scattered prostrate willows and a few grasses such as *Calamagrostis purpurascens.* No naturally occurring trees grow in the Aleutians although on Unalaska and Unimak there are scattered thickets of shrubby alder.

Characteristic of highland terraces and exposed points of land overlooking the sea are mounds which are steep-sided and conical, or rounded, and often 6 feet or more in height. In topography they may resemble middens, but excavation reveals them to lack human remains. These are bird-mounds (Fogletuer of Norwegian coasts); they have been formed through centuries from vegetation growing in the excrement of seabirds. Their vegetation has little in common with village mounds and human refuse heaps but is predominately made up of *Carex macrochaeta, Festuca* spp., *Poa* spp., *Trisetum spicatum,* the lichen *Sphaerophorus globosus, Lycopodium* spp., *Sphagnum* spp., and other mosses. A knowledge of this may save archaeologists a few hours of needless digging and the disappointment of finding only a large boulder at the bottom of an otherwise important-looking mound.

It is apparent from remains of old villages and from what we know of Aleut life at the time of Russian discovery that the island people were truly maritime and seldom ventured into the higher interiors of their islands. Only one village was located any distance from the sea, and it was distant only verticaly from the shore. It was observed on Agattu from the air. Consisting of a ring of small barabara pits in a circle about one much larger pit (possibly a kazim?), this village was situated atop a very high plateau with steep rock cliffs on three sides reaching to the sea below. The fourth side was a steep, heath-covered (?) slope decending toward the interior of the island. The

inhabitants must have had most difficult access to the sea but an almost impenetrable bastion of defense. It is not impossible that the village was once at sea level and the land has risen. Inasmuch as the Aleutian islands have undergone considerable uplifting in fairly recent times (U. S. G. S. 1947), it is conceivable that the oldest villages may not be near the sea at all but must be sought on the higher terraces, which for the most part have not been explored archaeologically.

Aleut Plant Uses

The plant lore of the Aleuts was once quite extensive according to information obtained from living natives and from perishable detritus in archaeological sites. The main body of ethnobotanical data will be published later, but briefly, the Islanders used more than sixty local plants for food, drink, medicines, and in the manufacture of such articles as grass mats, baskets, boat frames, etc. Beach pea (*Lathyrus maritimus*), and such grasses as *Elymus, Bromus,* and *Calamagrostis,* as well as some *Carex,* were used in weaving. Cow parsnip (*Heracleum lanatum*) and other of the Umbelliferae (*Conioselinum gmelini, Ligusticum hultenii, Angelica lucida*), as well as spring beauty (*Claytonia sibirica*), fireweed (*Epilobium angustifolium* var. *macrophyllum*) and many of the sea weeds (*e.g., Ulva* and *Fucus*) were extensively used by the Aleut for food. Roots of the lupine (*Lupinus nootkatensis*), black lily or riceroot (*Fritillaria camtschatcensis*), and the white orchid (*Platanthera,* several species) were used in various ways to supplement the fish diet. Leaves, stems, and roots were usually eaten raw and often were added to fish, berries, and water to make an uncooked fish "soup." Such plants as ragwort (*Senecio pseudo-arnica*), the common yarrow (*Achillaea borealis*), and the marsh-growing *Matricaria matricarioides* were known to be strong medicines.

From driftwood on the beaches, the Aleut fashioned boat frames, supports for the semisubterreanean houses, and lances. *Taxus, Picea,* and *Chamaecyparis* were the principal woods used. Cedar (*Chamaecyparis*), which drifted from the American Mainland, was carved into masks and shamanistic objects. The roots of monkshood (*Aconitum maximum*) were ground by some Aleut groups to extract the poison, which was then applied to harpoon points for whale hunting. As is true of this practice, much of the use of local plants has disappeared among the surviving Aleut.

It is apparent that the early Aleut never had to wander very far inland for useful plants. The majority of species which were used are readily accessible in the lowland meadows, stream valleys, marshes, and along the sea shore. Berries are plentiful in *Empetrum* mats which are never very far from village locations. It is striking that the characteristic plants today occurring on long abandoned village sites were all at one time used by the Aleut. *Heracleum, Conioselinum, Ligusticum, Angelica,* and *Claytonia* were used for food. *Achillaea, Heracleum,* and *Ligusticum* were mainstay medicines, and *Aconitum* was used as a whale and fish poison. *Elymus* was the primary source of weaving material.

It has been shown that *Elymus* and *Claytonia* frequent the hummocks and old terraces behind the shore line. *Claytonia,* but not *Elymus,* is also sometimes found in a loose association of *Conioselinum, Ligusticum, Heracleum,* and *Angelica* in lowland stream valleys. *Achillaea* may be found on the steeper banks that are drained and also with scattered growths of *Heracleum, Conioselinum,* and *Aconitum* in lowland meadows. The Aleuts used all of these plants; today they are found closely associated on abandoned village sites, but are otherwise from several differing habitats. This suggests a direct human influence on the vegetation of old villages, and this influence may be the primary historical factor

which determined the particular combination of plants on these sites.

Use of Vegetation in Archaeological Reconnaissance

This ecological study of old villages gives a method of locating such sites not only by surface exploration but also by aerial reconnaissance. During several flights across the entire Archipelago at low altitudes, it was possible to locate and map a large number of hitherto unreported villages. This information will be invaluable to future archaeological work in the Aleutians and will be published in the near future.

When viewed from the air, old Aleut villages present a unique appearance, being seen as dark green areas against the lighter greens and yellows of the surrounding vegetation. This is explained by the greater abundance of tall dark-colored plants such as *Aconitum* and *Heracleum* on the sites as compared with the lower-growing plants which prevail on non-village areas. From the standpoint of lushness and greeness of vegetation, many valleys and stream margins show the same dark green coloration, although not as sharply defined and hence usually not mistaken for archaeological sites. The lateness of season to which *Heracleum* and *Aconitum* retain their dark greeness gives to the margins of old villages an especially sharp delimitation in the early fall when the surrounding meadows and bogs have already taken on the yellow-orange coloration of winter. A strikingly distinctive feature of most village sites is the occurrence of depressed circular barabara (house) pits. These are likely to be choked with a heavy plant growth (as indicated in Figs. 3, 10), as well as being sunken, so that they are easily discerned even from high altitudes (Fig. 11).

There are already enough data at hand to determine not only the exact locations of old villages from the air but also,

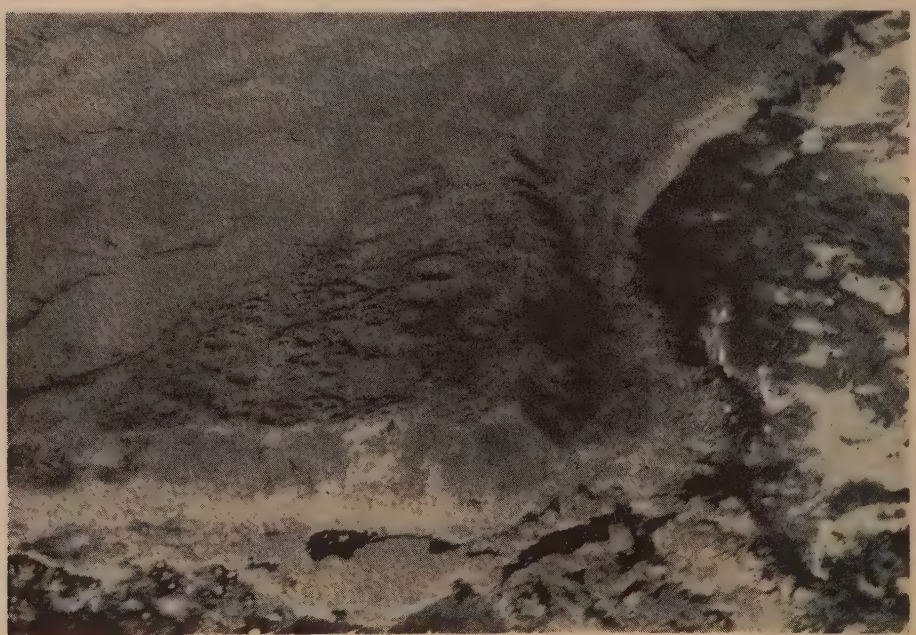

Fig. 11. Prehistoric Aleut village on Attu Island as seen from the air in September, 1949. Approximately 90 barabara pits can be counted, including several larger depressions which may have been community dwellings or possibly kazims.

roughly, their approximate human populations. In this latter respect, it is usually sufficient merely to pick out the surface areas of old sites by noting the sharply defined color patterns and counting the easily discerned barabara pits. There is every indication that a close evaluation of the factors influencing plant growth on and off such areas in the Aleutians will bring forth a usable scale for giving rough determination of the age of old villages by the vegetation occurring on them. The lushness of the house-pit vegetation is quite certainly to be related to the richness of deposits of fish bones and other fertilizing materials in the barabaras. This richness is undoubtedly related in turn to the age since abandonment of the sites.

Summary and Conclusions

There seems to be a definite correlation shown on former Aleutian village sites between plant growth and soil pH and these in turn, are influenced by elevation, drainage, and subsurface archaeological remains of fertilizer value, such as fish and mammal bones. Through the interaction of the above factors and others which are unknown, a definite, easily discernible, plant association occurs on old villages that is not duplicated elsewhere. Although the same plant species occur separately and to some extent associated in localities removed from human habitation, such as lowland stream valleys, there is never the same degree of association between, *e.g., Elymus* and *Heracleum,* as on village sites. In addition, the density of growth and lushness are usually less on non-village areas. The increased availability of certain nutrients, notably calcium, phosphorus, and possibly nitrates, in the midden soils is probably the main ecological factor determining these vegetational differences.

Aside from the factors of pH, drainage, elevation, and sub-surface deposits as reasons for the characteristic plant association on old villages, it is suggested that past Aleut plant economy may have been a factor. Every characteristic plant species occurring on the village areas was widely used by the Aleut as a source of food, medicine, poison or weaving material. Utilization was probably centered at the individual villages where undoubtedly the waste parts, especially the seeds, accumulated in abundance, establishing a ruderal vegetation which persists on the abandoned sites today.

The association-segregate, which I call the particular plant grouping on old villages, is evidentally made up of two, possibly more, separate plant communities, which, however, are not always distinguishable on every old village site. *Heracleum* and several other plants occur frequently as a single community within house pits, whereas *Elymus* and other grasses, sometimes with *Achillaea,* dominate pit margins, hummocks and the peripheries of villages, forming a somewhat distinct community. The details of this distinction are not sufficiently clear at present to allow a more complete discussion, but the many sensitive ecological factors which operate to determine these and other differing microhabitats on the ancient villages are certainly worthy of further consideration.

Identification of old villages from the air is easy, especially during the early months of fall and spring when the vegetational differences stand out with spectacular clearness. By aerial reconnaissance, which in the Aleutians is the most practical, the archaeologist can locate and map sites on the islands ranging across the entire Arc, including the Alaska Peninsula. It is possible not only to ascertain size and position of the sites from the air but also in most cases to count the numbers of barabara pits. This may even be done from photographs.

The problem now is not where to find villages for Aleutian archaeology but rather one of careful reconnaissance by air to locate and map the largest, most easily reached, and most productive-looking sites. Such a survey would not entail a great amount of time or money, provided military aircraft regularly flying

this route could be utilized. It should produce valuable data upon which could be based a plan for intensive, careful archaeology in the Aleutians during the next few decades.

It is possible that additional work on this problem will reveal a correlation between surface vegetation and age since abandonment of the villages. Such a correlation would seem to exist since the recently disturbed sites, such as Eider Point, present a denser vegetation than do villages abandoned longer, although it may prove too tenuous a relationship to be of practical value to the archaeologist. It may be a relatively temporary cultivation effect, resulting from improved aeration and the bringing of fertilizer nearer to the surface. The depth of leaching out of fertilizer constituents since abandonment might provide the reason for a correlation of vegetation differences with antiquity, if such differences can actually be discerned and measured.

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THE ECOLOGY OF THE DESERT IGUANA *DIPSOSAURUS DORSALIS*

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INTRODUCTION

The genus of iguanid lizards known as *Dipsosaurus* is a small group of medium-sized, rather robust forms found in southwestern North America. The genus is related to the genera *Ctenosaura* and *Iguana*. The resemblance is striking when the young of each of these genera are compared. Like others of this group, *Dipsosaurus* has a mid-dorsal longitudinal row of enlarged scales, but unlike the most closely related genera, the scales are not greatly produced into a crest in adult males. I have adopted the vernacular name *desert iguana* for *Dipsosaurus dorsalis*. The ecology of the lizards of the genus *Dipsosaurus* is very poorly known although it is one of the most common desert creatures in the southwestern United States and western Mexico. Smith (1946), in discussing the United States form, *Dipsosaurus d. dorsalis*, says: "Almost nothing is known of the breeding habits and life history of this species." Equally little is known of the Mexican forms. Opportunities to observe *Dipsosaurus* were afforded me during the spring and early summer months of 1947–50. Observations were made over most of the range of the genus, including Baja California, Sonora, California, Arizona and Nevada.

The dorsal color pattern of *Dipsosaurus* is composed of a black or brown reticulum superimposed over a white or pinkish background, sometimes forming definite longitudinal lines, indefinite vertical bands, or rounded or irregular ocelli (Fig. 1). The ventral surface of the desert iguana is usually white or grey. During breeding season both males and females show longitudinal latero-ventral patches of pinkish grey, brownish red, or brownish orange. The coloration of these patches and of the dorsal markings is quite variable geographically, there being marked adaptation of dorsal coloration to soil color in some localities (e.g., Algodones Dunes, Imperial County, California).

The lizards of the genus *Dipsosaurus* occupy lowland habitats at least as far

FIG. 1. *Dipsosaurus dorsalis dorsalis*. An adult female from Borego Desert, San Diego County, California. Loaned through the courtesy of Messrs. C. B. Perkins and Charles Shaw, of the Balboa Park Zoo, San Diego, California. Photo by James Rupert.

south as Ahome, Sinaloa (Bogert and Oliver 1945, p. 401) on the mainland of Mexico, and to Cabo San Lucas on the peninsula of Baja California. Northward the genus is found in the desert areas of western Sonora and Baja California, through the western half of the Arizona deserts, into southern Nevada and southwestern Utah (Woodbury and Hardy 1940). In California the desert iguana ranges as far north as the southern Great Basin in Saline Valley, Inyo County (Miller 1944). Klauber (1929) and Bogert (1930) report the presence of *Dipsosaurus* in the San Fernando Valley, of Los Angeles County, California. Bogert (personal communication) doubts the authenticity of this record. He says it was based on a specimen sent in to the old Herpetological Society of California, and judging from its appearance may have come from a Lower California locality. Klauber (1939) likewise suggests that this record be suppressed. At any rate it is almost certain that no *Dipsosaurus* occurs today in the densely populated San Fernando Valley, the known western limit of the genus being in the vicinity of Last Chance Canyon, Kern County, California, on the Mojave Desert.

Many of the life history data presented here are fragmentary because few observations have been made during the late summer months.

I wish to express my appreciation to Raymond B. Cowles, under whose thoughtful guidance this study has been conducted. Sarah R. Atsatt has supplied information and observations related to several parts of the study. Several persons have aided greatly as field companions and collectors and have helped develop many of the ideas of this paper while sitting around the camp fire. First, my thanks to Charles H. Lowe, Jr., and his wife Arlene. I wish also to thank Richard G. Zweifel, William G. Reeder, William Bittle, and Conrad Limbaugh in this regard. C. B. Perkins and Charles Shaw have critically reviewed the manuscript. I wish to express my thanks to Sam Hinton, who prepared the illustrations. Finally special thanks are due to Mr. and Mrs. Renaud Hoffman who generously allowed me to use their new home as a sort of desert laboratory during the summer of 1948.

Habitats

In the United States, northern Sonora and northeastern Baja California, *Dipsosaurus* is totally restricted to desert areas. In the southern portions of its range the lizard lives in arid subtropical scrub and short tree forest associations. It is often exceptionally abundant in these subtropical regions.

The habitat in which the southern segments of the genus live is thought to be of considerable antiquity (Axelrod 1948). The deserts are relatively new features and are considered to have developed during Pliocene and later time (Axelrod 1950). During the Cenozoic, aridity reached a climax in the Middle Pliocene, producing rather extensive areas of semidesert conditions. Arid subtropical scrub vegetation was rather widespread at this time and covered much of the area now occupied by *Dipsosaurus*.

In the deserts, *Dipsosaurus*, like all other reptiles of these regions, lives in a small segment of the entire available climatic habitat. Selection of this portion of the total range of habitat conditions (here called a partial environment) is achieved by various adaptations to be discussed later. The partial environment in which desert populations of *Dipsosaurus* live today approximates the present climate of arid subtropical scrub regions. The lizard avoids both extremes of heat and cold in desert climates. It is apparently much more ubiquitous in the arid subtropical scrub habitat. The limiting effect of desert humidity ranges is more difficult to assess. The body temperature range within which *Dipsosaurus* is active has the highest recorded maximum of any lizard in North America (46.4° C;

see *Temperature,* below), which, while unique, is far below normal spring and summer habitat extremes. On the deserts the lizard lives in a hot, arid partial environment, without great extremes of heat or cold.

The fact that the selected partial environment of desert *Dipsosaurus* is much like the overall climate of arid subtropical scrub regions suggests that the desert iguana spread over the present desert regions with the older flora and remained, by virtue of a measure of preadaptation, as desert conditions developed.

Soil Types

Sandy washes are often occupied by dense populations. The arroyo at San Ignacio, Baja California del Sur, Mexico, supports a particularly large population. On July 22, 1949 at 8 A.M. Charles Lowe, Jr. and I crossed the arroyo, over a partially cleared stretch of land dotted with mesquite thickets, stumps and piles of limbs ready to be burned. Lizards were extremely numerous. *Callisaurus draconoides, Uta stansburiana, Sceloporus magister rufidorsum* and *Dipsosaurus dorsalis* were everywhere. Sometimes 7 or 8 lizards could be seen running over the sandy arroyo at once. *Callisaurus* was the most abundant, comprising about two-thirds of the lizards seen. *Dipsosaurus* was next in abundance, composing somewhat less than a third of the lizards seen. In half an hour about 20 *Dipsosaurus* were noted racing through the mesquites and fallen palm fronds.

This wash is periodically subjected to violent flooding, a fact attested to by the massive earth and rock flood diversion wall (now in disrepair) constructed across the arroyo under the direction of the Spanish Jesuit Padres during the 1700's. Nelson (1922) reports that many small houses in the arroyo were destroyed by flood in 1911. Probably minor floods are a common occurrence and this dense lizard population must re-establish itself from time to time.

Dipsosaurus d. lucasensis occupies stream bottoms in many places. It was noted at San Bartolo, Baja California del Sur, on the sandy floor of a deep rock-walled arroyo. When frightened it took refuge in rock crevices. At La Burrera, inland from Todos Santos, in the foothills of the Sierra Laguna, the lizard lives in a dense jungle of plants along the edges of a dry stream bed in the bottom of a deep granite canyon. On the La Paz plain *Dipsosaurus d. lucasensis* was most common in open areas and along the edge of washes. This plain is densely covered with subtropical scrub composed of short leguminous trees, giant cacti, elephant trees, and a dense tangle of vines.

On the Magdalena Plain, Baja California del Sur, Mexico, *Dipsosaurus* seemed to be almost entirely restricted to the edges of sandy washes. It was also noted that the creosote bush (*Larrea divaricata*) was much more common in this niche than elsewhere.

One of the densest populations of *Dipsosaurus* noted by the author is located along the western edge of the river valley at San Jose del Cabo, Baja California del Sur. Here the animals occupy sandy soil strewn with boulders, sparsely covered by thorn forest vegetation. At this location on July 9, 1949, 20 individuals were noted on or near the road in one-quarter of a mile.

Northern *Dipsosaurus* populations seem to be most dense in areas of wind-blown sand anchored by creosote bushes. Desert iguanas are common over most of the dunes of the Coachella Valley, Riverside County, California. They occur in similar habitats at Daggett, Harper Lake, Bristol and Cadiz Lakes, Sperry Canyon, Crucero Flood plain, and Cronise Dry Lake, all in San Bernardino County, California. *Dipsosaurus* is common, almost to the limit of vegetation, on the huge Algodones Sand Hills of Imperial County, California. Similar populations occur on the dune portions of the Gran

Desierto in northwestern Sonora, at El Papalote, and Tepoca Bay, Sonora. Probably all suitable dune situations within the range of *Dipsosaurus* harbor populations.

Dipsosaurus commonly occurs on soil types other than sand though population densities are nearly always much less in such cases. At Pichacho, Imperial County, California, individuals were captured on very rocky soil. One specimen was dug from a burrow in the edge of a rocky stream bank. Another individual was taken from a similar burrow in rocky soil at Willis Palms, Riverside County, California. In both cases the burrows were shallow and consisted of excavations under the roots of creosote bushes. Desert iguanas have been taken from the boulder-strewn Chino Canyon alluvial fan, which washes out onto the floor of Coachella Valley near Palm Springs, Riverside County, California. One individual was seen perched on top of an 8 foot granite boulder near the foot of this fan. The lizard does not occur far up the canyon but is restricted to the lower portions where areas of coarse soil and some sand are interspersed among the rocks.

Areas of clay soil are commonly inhabited by *Dipsosaurus*. At several locations along the banks of the Colorado River the lizard is common on clay river terraces. Numerous individuals were seen on hard-packed clay soil at the Cape of Baja California, between San Lucas and San Jose del Cabo.

The flood plain of the Rio Yaqui, in southern Sonora, Mexico, supports scattered populations of *Dipsosaurus*. The lizard is common in some localities and absent in others, seemingly occupying areas of high ground. Here the desert iguana lives on clay or sandy soils and usually retreats to dense thickets of *Opuntia* or *Fouquieria* when pursued.

Dipsosaurus seems restricted to areas in which soil conditions allow the construction of burrows, either by the lizard itself, or by various species of mammals (chiefly *Dipodomys* and *Citellus*). The genus occurs in considerable numbers in areas subject to transitory flooding but does not occupy areas in which standing water covers the land for any considerable length of time.

Plant Associates

Throughout most of the range of the genus the dominant plant associate is the creosote bush (*Larrea divaricata*). The flowers of this plant furnish a large proportion of the lizard's spring food supply and the bush is used for shelter from predators and excessive heat during all of the active season. *Dipsosaurus* usually hibernates in burrows constructed among its roots. In fact *Dipsosaurus* may be so closely associated with this bush that pattern adaptation has taken place. When the excessive heat of a desert spring or summer day forces these lizards to take shelter they often crawl in among the recumbent branches and roots of the creosote bush. At this time their banded tail pattern and mottled dorsal coloration make them all but invisible among the banded branches and patches of light and shadow.

Southward, creosote-bush desert gradually gives way to dense tangled arid subtropical scrub composed of numerous small thorny trees, large and small succulents such as cacti and elephant trees, and vines. It is doubtful that the desert iguana is closely associated with one species of plant in this region but rather is limited by soil conditions and humidity.

The southern limits of the range of *Dipsosaurus* seem to occur at the northern fringes of the short-tree forest. The characteristics of this forest have been defined by Gentry (1942). The short-tree forest is a "heterogenous deciduous forest with a strong infusion of tropical elements. It also alternates periods of growth with periods of dormancy, relative to the two wet seasons and the two dry seasons. Though it intergrades with

the Thorn Forest here called Arid Subtropical Scrub, it is in the aggregate distinguished from it by greater height, by larger leafage, by a greater proportion of mesomorphic and hydromorphic elements, and by the relative infrequency of thorny and succulent plants." In the foothills of the Sierra Laguna, Baja California del Sur, *Dipsosaurus* occurs in low concentration in the edges of such a forest. It occupies clearings and generally takes refuge in *Opuntia* thickets. What specific factor limits the southward expansion of the desert iguana is not clear but it is probably related to increased moisture as the tropics are approached.

Burrows

In past reports little mention has been made of the burrowing habits of *Dipsosaurus*. Burger and Hensley (1949) discussing *Dipsosaurus* in northern Sonora, Mexico, stated: "The lizards were very abundant in creosote flats where they quickly escaped into burrows beneath the creosote bushes. One burrow from which a *Dipsosaurus* was dug was a simple tunnel six inches deep and about a foot and a half from entrance to exit. Other burrows investigated were more extensive and more complex, extending down as much as two feet below the surface and sometimes three or four feet horizontally, with many entrances. The burrows appear to be abandoned mammal excavations."

Several authors (Camp 1916; Cowles 1920; Klauber 1939; Linsdale 1932; Johnson *et al.* 1948; and Van Denburgh 1932) have referred to the genus occupying burrows. In each case the burrows have been designated as mammal burrows or were unidentified. Cowles (1941) reported on a series of *Dipsosaurus d. dorsalis* excavated from hibernation. A number of juveniles were uncovered at depths from 2 to 6 inches; no juveniles were taken from depths greater than a few inches. Some adults were found *in situ* in small cavities from 2 inches to 2 feet below the surface. Cowles indicated that the desert iguana does not often use mammal burrows for hibernation but instead occupies shallow excavations.

During the active seasons *Dipsosaurus* generally makes use of mammal burrows when they are readily available. Pairs and even three individuals have been observed to retreat to the same *Citellus tereticaudus* burrow. The burrows of *Dipodomys deserti* are often frequented. It is not known whether these burrows are sometimes also occupied by the mammal. Both juveniles and adults have been observed to inhabit mammal burrows.

In some areas mammal burrows are scarce and it is there that burrows constructed by the lizards themselves are most often found. The dunes between Palm Springs and 1000 Palms Junction, Riverside County, California, are a good example of such a situation. At this location on July 9, 1948, an adult male *Dipsosaurus* was observed sunning by the mouth of a 1–1/2 inch hole, about 30 feet from the nearest creosote bush. When the animal was approached he quickly entered the burrow. Excavation revealed a chamber (see Fig. 2) 2–1/2 inches beneath the surface. This chamber was roughly oval and about 3–1/2 inches in length. Two additional entrances were found, each plugged at the surface by about 2 inches of sand. The animal was marked and released. My companion and I remained at the edge of the burrow writing notes. The lizard ran a few yards away upon release and then returned to within two feet of me. After a few moments of indecision the animal ran between us and re-entered his partially excavated burrow. The animal was very light in color (cloacal temp. 42° C). It seems probable that he was seeking retreat from the hot surface temperatures (sand surface, 42.0° C, air at 1 cm, 37.6° C on the flat). The sand temperature at the bottom of the burrow was 35.2° C.

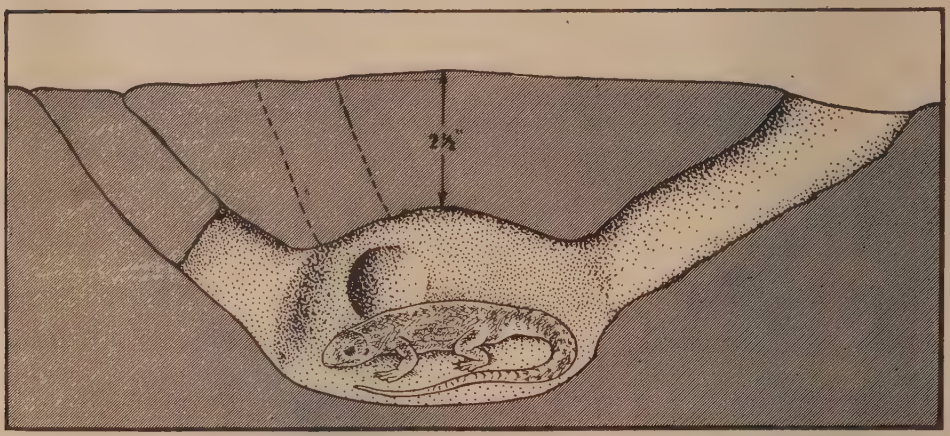

FIG. 2. A typical burrow of *Dipsosaurus* dug in sand east of Palm Springs, Riverside County, California.

Other burrows have been excavated that apparently were dug by *Dipsosaurus*. In general they are shallow and located under bushes. Two such burrows have been excavated in rocky soil. These burrows were both very shallow, the roof of each being about 1/2 inch thick.

Juveniles construct burrows that are proportionately smaller and shallower than those of adults. Several individuals have been excavated from very shallow burrows. A typical juvenile burrow was investigated on September 27, 1948, between Palm Springs and 1000 Palms Junction. A juvenile desert iguana was seen entering a small hole beneath a spreading bush (*Dicoria canescens*). When excavation was started the lizard popped out of the far end of the tunnel through a thin surface layer of sand, ran past two bushes and directly to another similar burrow, 35 feet from the first one. Both burrows consisted of small tunnels about 1–1/2″ deep and 12″ long, with one entrance open and the other blocked by a thin layer of sand. None appeared to have a central chamber.

These shallow juvenile burrows doubtless offer rather poor protection against winter cold. Possibly *Dipsosaurus* is limited on the northern fringes of its range and at high altitudes [1] by excessive juvenile mortality incurred because of this poor shelter. Cowles (1941) says of hibernating desert reptiles: "It is surprising to find cold-sensitive animals selecting dens at depths where they are subjected to fluctuating as well as to extremely low temperatures, while much more moderate conditions prevail at a readily accessible depth near-by."

At 10:30 A.M. on July 14, 1948, in the Coachella Valley dunes near Palm Springs, an adult male desert iguana was noted resting in the shade of a large sprawling creosote bush. By 11:15 A.M. air temperatures near the surface of the sand underlying the bush were near 45° C (see Fig. 5B). The lizard was gone. His tracks revealed that he had left the bush and gone straight to the next one northward, a distance of about 50 feet. He had gone directly around the north edge of the bush and entered a burrow hidden at its base. The sand around the burrow entrance was smoothed of all tracks. Repeated observations of the

[1] Johnson *et al.* (1948) list 3,200 feet as the maximum at which they took desert iguanas in the Providence Mountains region. This is the highest altitude record for the genus, to my knowledge.

smooth sand showed that the lizard did not leave the burrow until mid-day heat began to abate. Between 3:30 and 5:30 P.M. tracks on the sand showed that the iguana had come out, made a short sortie, and reentered the burrow. The burrow was visited during the night and found closed by a plug of sand two inches thick. A strong wind carrying considerable sand was blowing over the dunes at the time, making it impossible to tell whether the entrance was closed by the animal or by wind-blown sand. Caged *Dipsosaurus* have been observed to block their burrow entrances at night. One adult female burrowed in a deep sand pile and plugged the entrance of her burrow by piling sand in it with her front feet. The burrow produced by this animal consisted of one exit tunnel (usually plugged when the animal was inside) and a chamber about two inches high by four inches long. The lizard emerged after a heat lamp was turned on the entrance. She pushed through the loose sand in the exit and lay sunning with only her fore parts exposed for a short time and then emerged completely. The selective advantage of plugging burrows at night is obvious. Such a habit would certainly offer some protection from nocturnal predators such as the glossy snake, *Arizona elegans* (see Cowles 1941).

Home Range Behavior

Some of the examples cited above give clear evidence that both juveniles and adults occupy home ranges, at least during late spring and early summer. Often when pursued, desert iguanas will run past suitable-appearing hiding places and go directly to burrows that are hidden from view. This observation has been made so often that there is little question that these lizards have a specific home burrow or burrows to which they regularly retreat.

Aggressive Behavior and Territoriality

During part of the seasons of activity *Dipsosaurus* is more or less gregarious, many lizards congregating in areas where food is abundant (see *Food Habits*). Breeding males establish and defend territories during the mating and post-mating periods (May, June and early July). One territorial defense was observed on July 15, 1948, on the Coachella Valley dunes. An attempt to capture an adult male caused the animal to run from its sheltering bush across an area of open sand to a group of creosote bushes. As this lizard approached the bushes another adult male rushed out of them, his flanks laterally compressed and his body arched. He stopped twice, did "push ups" and threw out his gular fold, and then chased the intruding male for about 25 yards into another clump of creosote bush. He then gave up the chase and returned to his bush. Both animals were captured and proved to be males in breeding condition though the breeding season was over and spent females were emerging from egg laying at the time. Their body temperatures were 43° C (intruder) and 42.7° C (aggressor).

Display has been observed in adult males in the laboratory and consists of a lateral flattening of the body and extension of the gular fold. Some animals produce a raised longitudinal mid-dorsal roach (see Fig. 3), thus further increasing their frightening lateral proportions. The fighting observed in the laboratory was confined to intimidation, with no contact being made. R. B. Cowles (pers. comm.) has observed contact during aggressive behavior and has kindly supplied the picture (Fig. 3). These two animals were observed just south of Mecca, Riverside County, California, during May. Both proved to be males in breeding condition.

It is possible that the seasonal latero-ventral reddish band of breeding animals

is important in this display. Noble and Curtis (1939) have pointed out that the breeding colors of male jewel fishes (*Hemichromis*) make specific movements, which act as releasers, more conspicuous, and thus aid in courtship and sex dis-

FIG. 3. Aggressive behavior between two *Dipsosaurus d. dorsalis* males, taken halfway between Mecca and the Salton Sea, Riverside County, California, by R. B. Cowles. Notice the mid-dorsal longitudinal roach raised along the back of the right hand animal. When first observed the animals were thrashing around on the road. One was bleeding from its flank and its tail had been broken during the fight.

TABLE I. *Reproductive cycle of* Dipsosaurus dorsalis dorsalis

All animals examined for this table were adults or yearling animals (snout-vent length over 100 mm), captured in California, Arizona and Nevada. Records of females for the months of May, June and July are segregated into those taken before and after the 15th of the month. The female group is also divided into what probably represents animals with maturing and non-maturing ova. Note that animals with non-maturing ova predominate greatly through June and July. See text.

Month	No. animals	Range of testis size	No.	Ova size	No.	Ova size
February	1	2 mm	—		—	
March	4	2–6 mm	—		—	
April	6	8–14 mm*	5	1–2.5 mm	2	3–4 mm
May	19	7.8–12.3 mm	5	2 mm	4	6–8 mm 15th
			4	2 mm	1	10 mm
June	17	10–12.5 mm	6	2 mm	3	10–12 mm 15th
			9	2–5 mm	3	10–20 mm
July	27	6.5–11 mm	12	2–4 mm	3	17–35 mm 15th
					2	8–19 mm
August	—	—	—		—	
September	7	6.0–7.0 mm	4	2–4 mm		

* April 6, 1947, Death Valley, Calif., UCLA 3037.

crimination (see also Tinbergen, 1948). The lateral display of *Dipsosaurus* males probably serves similar functions and is enhanced by the breeding coloration. Such coloration would certainly make the animal's body outlines more distinct to a prospective mate or an invading male.

YEARLY ACTIVITY CYCLE

Dipsosaurus emerges from hibernation later than most other desert lizards; this probably is a function of its high temperature requirements. Emergence usually occurs in middle or late March, in the Coachella Valley area. In 1948 the first individual was noted on April 3, though desert iguanas probably commenced emergence a week or two earlier when no observations were made. The earliest date of capture noted for museum specimens is March 18, 1941.

Adult male *Dipsosaurus* show an increase in testis size until about the beginning of April (see Table I). Complete recession of the gonads does not appear to take place in all males until late summer. This maintenance of enlarged gonads in some or all males probably accounts for the occasional aggressive behavior exhibited after the mating season has been completed.

During spring and early summer female desert iguanas may be segregated into two classes, those whose ova increase beyond 2–4 mm in length and those whose ova remain minute throughout the spring and summer. This must be a function of fertilization or maturation of ova. Exactly when the peak mating period occurs is not clear. However, the sharp break between these two classes of females becomes apparent early in May (see Table I). Females with enlarged ova have been found abroad as late as July 20th.

During middle and late June and early

July the percentage of gravid females in the total population drops sharply. At this time most females with developing eggs retreat underground and do not reappear until the eggs have been laid. A fertilized female (snout vent length 129.5 mm (UCLA 687)) was kept in captivity by Robert R. Miller from May 29, 1937 until June 23, 1937 when 7 ova were fully developed (30–35 mm × 19–21 mm) and so distended the creature that its movements must have been seriously hampered. The animal died in captivity without laying its eggs. I captured such a distended female on July 2, 1948 containing shelled eggs ready to be laid. Similarly in this case the animal was so enlarged as to be hampered in locomotion. Probably most female *Dipsosaurus* retreat underground not only to lay their eggs but to gain shelter at a most vulnerable time. Lizards with small clutches seem to retain normal locomotion during development of the eggs. Clutch size is from 3 to 8 eggs.

During the period when egg-laying females are underground, females with undeveloped ova remain on the surface and may usually be seen in the company of a male lizard. These females may be yearling animals which are not yet reproductively competent. Pairing continues until mid-July. Early in July the spent females begin to emerge. They are much emaciated and usually undergoing shedding. Their powers of temperature control seem somewhat reduced (see *Temperature and Humidity*).

Young *Dipsosaurus* emerge through August. By fall (late September and October) these young animals are by far the most common age group in evidence. Probably adults go into hibernation quite early in the fall. The small animals are able to take advantage of shorter stretches of favorable weather than are the larger adults because of their ability to reach activity temperatures more quickly. Perhaps this is the factor which allows them to be active while their parents must retreat underground.

Hibernation occurs in burrows of various depths. Probably most of these burrows are constructed by the animals themselves. Cowles (1941) found adult *Dipsosaurus* hibernating at depths of 2 to 20 inches. Most animals were found 4 to 6 inches below the surface. He says: "Five other juveniles were obtained from shallow excavations estimated as 2 to 6 inches from the surface. No juvenile could be assigned to greater depth than a few inches below the surface. . . . All the juveniles from hibernation were emaciated, feeble in their motions even when warmed up, and none was robust enough to survive the change from hibernation to an active life in the cage. The adults survived in all cases, except where they had suffered mechanical injury from the passage of the scraper blade."

Problems Relating to Temperature and Humidity

The relative importance of temperature, humidity and light in regulating the distributions and activities of reptiles varies widely in different ecologic situations. The manner in which each of these factors acts is often quite cryptic in more mesic environments. The extreme environment of the desert throws some of these relationships into sharp focus. Not only are temperatures of the North American deserts often very high but the diurnal range of temperature is usually great. Humidity ranges are also great. Generally, hygrophilous forms are restricted around the periphery of deserts or invade by occupying severely restricted partial environments concentrated around areas of permanent or temporary water. The latter case is typified by the genus *Scaphiopus* which, on the deserts, emerges from inactivity only during the infrequent rains; its entire reproductive cycle is geared to these irregular periods of moisture.

The interplay of humidity and temperature in controlling the activities of diurnal desert lizards is poorly under-

stood. Both factors are doubtless of great importance. Of the two, the effects of humidity are far more obscure. In the extreme deserts occupied by *Dipsosaurus* one can measure with surprising precision the onset of limiting temperatures but the effects of diurnal shifts in humidity upon lizard activity are not so easily demonstrated. Probably humidity is a controlling factor in summer aestivation, if such occurs in this genus. Lizards and snakes may be forced below ground by seasonal desiccation. The often-observed increases in reptile activity following summer rains are another expression of humidity. It is probable that desiccation during winter hibernation kills many individuals at times. Desert iguanas which have just emerged from winter hibernation are often emaciated and quite probably in a state of desiccation as well. In the northern portions of the range of *Dipsosaurus* extremely dry spring conditions may cause a considerable mortality of juveniles and adults alike during the critical period of emergence. Cowles (1941) pointed out that lizards hibernating in shallow burrows will be much more readily affected by air temperatures when the soil is wetted by rains than through dry soil. Juveniles in their shallow burrows might be subjected to killing temperatures in this way. In this regard it is interesting to note that the northern limits of the genus are in an area of winter rainfall.

The adaptive problem of living in an arid environment where no rain may fall for 15 months or more has been "solved" by diverse reptilian types. No cold-blooded vertebrate has "solved" the problem of occupying, more than temporarily, a micro-environment where habitat temperatures daily exceed 50°C. During the summer *all* active reptiles and nearly all endotherms retreat and emerge almost daily, in relation to physiologic temperature tolerances. These cyclic activity periods await the study of any ecologist who wishes to match tolerances with the desert animals involved.

Of North American desert reptiles *Dipsosaurus* is able to remain active in hotter environments than any other genus. Johnson *et al.* (1948) state: "They [*Dipsosaurus*] foraged most actively during the hottest part of the day. Near Kelso, on June 20, 1940, they were first seen at 8 A.M. and remained active until 1 P.M., by which time lizards of other kinds (*Callisaurus, Uma, Cnemidophorus*) had disappeared."

Two classes of adaptations are of importance in the environmental temperature tolerance of *Dipsosaurus:* (1) behavioral and structural temperature regulatory adaptations, and (2) physiological adaptations to high temperatures. The first class includes such adaptations as behavior patterns which aid in temperature control and various morphologic features of the lizard which serve to protect the lizard from excessive temperatures. Behavior patterns and structure relating to temperature control will be discussed at some length.

The physiology of high temperature metabolism is not within the scope of this paper. Such problems offer an open field for some fascinating research. The only allusions that will be made to the physiologic tolerance of *Dipsosaurus* are contained in the data concerned with thermal activity ranges, temperature selection and in the brief discussion of ultraviolet radiation effects.

Behavior patterns related to temperature control

The hottest part of the micro-environment in which *Dipsosaurus* lives is the soil or sand surface. Two behavior patterns of the desert iguana seem to aid in resting on this hot surface. First, when the animal stops on hot sand it will often press its abdomen close to the sand and wriggle its whole body and tail from side to side. When unusually hot sand is encountered *Dipsosaurus* will usually begin shovelling movements with its front feet, at the same time moving forward

into the excavation with movements of the hind feet. This shovelling is accomplished by bending the front feet inward and pushing sand forward with alternate, rather violent thrusts of the palms.

Both shovelling and body-wriggling appear to be adaptations which serve to break through the hot surface layer of sand into the cooler strata beneath. Both of these patterns have been repeatedly observed in the laboratory and occasionally in nature. Shovelling marks can often be seen on the crests of sand hummocks from which a *Dipsosaurus* has been frightened.

Like most desert reptiles *Dipsosaurus* flexes its toes and elevates its tail when running or standing on hot surfaces. Unlike most other lizards it does not always elevate its abdomen under similar circumstances. Several times I have seen the desert iguana resting on hot sand, its abdomen slightly buried, its toes flexed (often the front feet are lifted entirely off the surface) and its tail arched above the sand. *Cnemidophorus* also exhibits this behavior pattern.

Dipsosaurus apparently remains above ground as long as any portion of its immediate environment offers tolerable temperature conditions. The lizard has been noted above ground even when only a very restricted portion of the shady side of the sand hummock was below 47° C (air and sand-surface temperatures). Under such conditions the lizard was always completely quiescent and unable to carry on normal feeding sorties. A rather definite cycle of activity has been noted in correlation with the cycle of daily habitat temperatures. In conjunction with attempts to define this activity cycle, records have been taken of diurnal temperature changes in the micro-environment of *Dipsosaurus,* at 1000 Palms Junction, Riverside County, California. Temperatures were taken around a sand hummock during the years 1948–49 at this location. In this area sand has accumulated among the branches of creosote bushes, forming regular-shaped hummocks. Strong, regular, north-northwest winds have oriented these hummocks and have truncated the deposits on the north-northwest side of the anchoring bushes. Fine sand is piled on the lee side of the bushes as a long low stringer. In this study temperature records were kept for a typical hummock about 40 feet in length. Fifteen stations were set up around the dune and among the anchoring branches (Fig. 4). Subsurface temperatures (2 cm deep), surface temperatures (the thermometer bulb was pressed into the sand but not covered), and temperatures 1 cm above the sand were taken at each station. In addition, readings were taken at various heights in the bush. In all cases the thermometer bulb was shaded with the hand while the record was taken, with care being used that the hand was not so close as to influence the reading. Records were made at approximately 3-hour intervals throughout the day. Duplicate readings were made on the same dune at about the date of spring emergence and near mid-summer when temperatures were close to maximum. A clear calm day was selected in each case. A slight breeze blew during the afternoon on which the

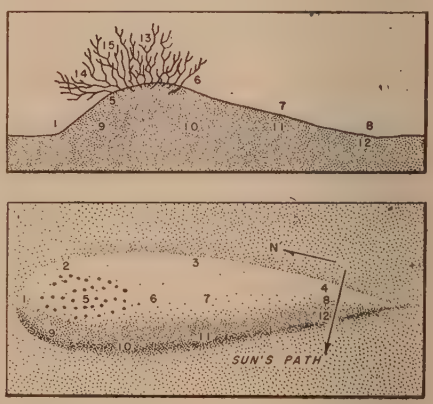

Fig. 4. Temperature stations taken on a sand hummock at 1000 Palms Junction, Riverside County, California. The anchoring bush is *Larrea divaricata.* The arrow indicates the sun's path across the dune.

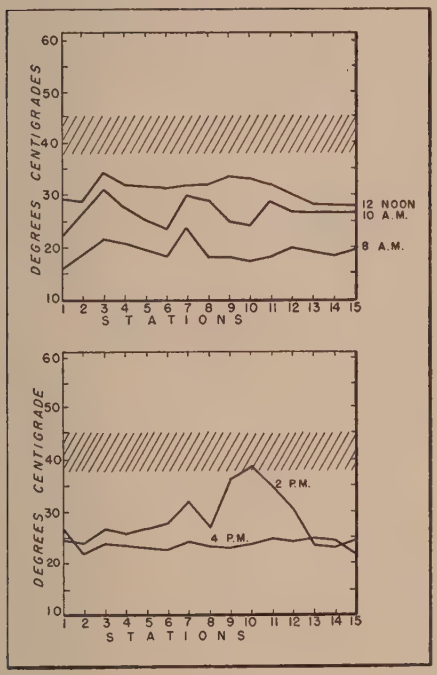

FIG. 5. Air temperatures, March 12, 1948. No air temperature shown exceeds the tolerance limit of *Dipsosaurus*. Most are well below the optimum temperature for the lizard and thus they must obtain most of their thermal supply at this time from the soil surface or from direct radiation.

July readings were taken. A Schultheis Cloacal Thermometer was used for all readings (Bogert 1949). This type of thermometer comes to equilibrium rapidly and thus reduces the length of time required to take each group of readings. This type of thermometer was also used for all cloacal temperatures listed in this study.

March temperatures are all below the maximum tolerated by *Dipsosaurus*. Early in the year (March and early April) the lizard is active throughout the middle of the day. Later in the season, over an increasing proportion of the habitat, midday temperatures rise above the maximum tolerated by *Dipsosaurus*. In mid-summer, temperatures are usually so high that the lizard remains above ground for only 3 or 4 hours in the morning. During these hours the activity of *Dipsosaurus* is strictly controlled by temperature. In the area of uniform sand hummocks at 1000 Palms Junction it is possible to predict with considerable accuracy where *Dipsosaurus* will be found at any time during the summer activity period. For example, the lizards generally avoid areas where soil-surface temperatures are in excess of 50° C and air temperatures over 45° C.

The daily passage of the sun over these regular sand hummocks creates a predictable series of thermal events in the niches of ground dwelling lizards such as *Dipsosaurus*. In the morning the sun warms the east face of the sand hummock

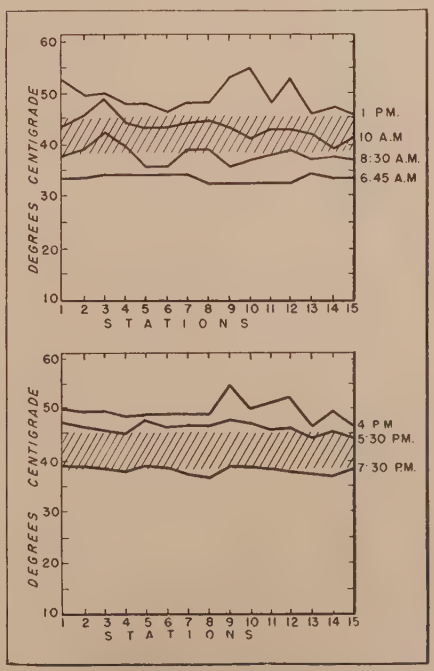

FIG. 6. Air temperatures, July 12, 1948. By 1 p.m. all air temperatures are above the tolerance limit of *Dipsosaurus* at all stations. Highest temperatures at each checking period occur in situations exposed to direct sun. Other stations are of relatively uniform temperature at any given time, this temperature becoming greater until late afternoon.

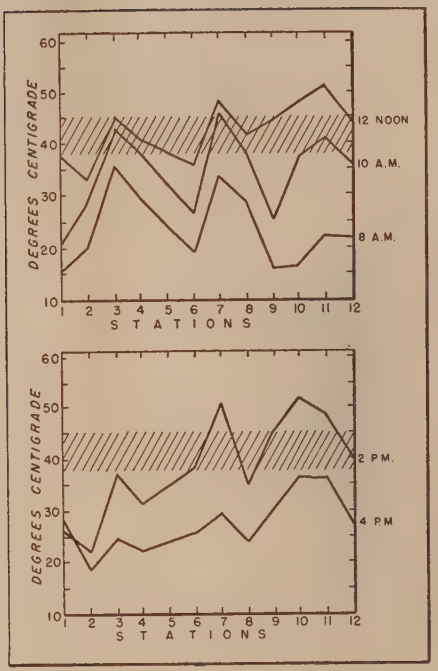

FIG. 7. Surface temperatures, March 12, 1948. Note that throughout the day there are always some stations at temperatures habitable to *Dipsosaurus*. As the day advances peak temperatures shift from one side of the dune to the other. Shaded area indicates the approximate activity temperature range of *Dipsosaurus*.

and the sand expanse between hummocks. The west face and the areas shaded by plants retain their nighttime temperatures until slowly warmed by the increasingly warm air. As the sun climbs higher, west slopes are warmed by the oblique rays of the sun. The more nearly perpendicular the sun's rays the greater the degree of warming. In general each location reaches its maximum surface temperature when the sun is perpendicular to it. The truncated north slope of the hummock never receives the full force of the sun. In addition, the surface layers of air have become heated by this time, and contribute, maintaining higher temperatures on the exposed surfaces and reducing cooling on the more protected east-facing slopes. The air over the dune is hottest at the surface and decreases in temperature upward. Air, being a fluid medium, does not show the extreme temperature differences of the soil surface but is much more uniform over the entire hummock (Figs. 5, 6). Because of this uniformity, on a hot day, all locations on a hummock may exceed the temperature tolerance of *Dipsosaurus* (Figs. 7, 8).

Subsurface temperatures do not reach their maximum at the same time the

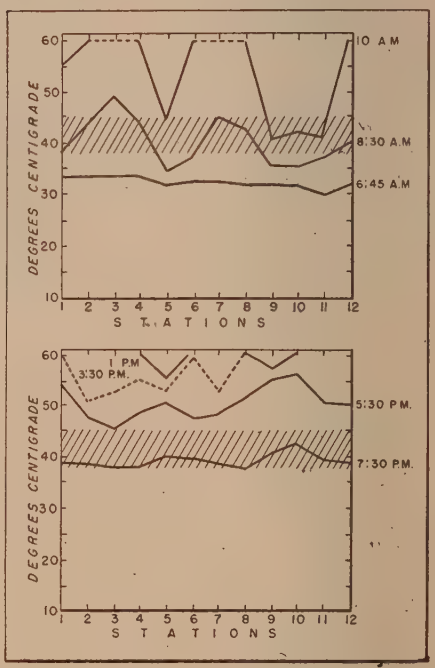

FIG. 8. Surface temperatures, July 12, 1948. 0645 a.m. temperatures represent unaltered nighttime surface temperatures. The summer sun quickly alters this uniform condition, raising the overall temperature by producing a layer of heated air over the dunes and by creating peak temperatures, in exposed stations, above the tolerance limit of *Dipsosaurus*. By 10 a.m. nearly all sand surfaces are heated in excess of this tolerance limit. By this time the lizards are controlling their body temperatures by various means. Later in the day, until near sunset, all surface temperatures are above the tolerance limit.

surface temperatures do but are delayed by the insulating properties of sand. The heat "soaks" into the sand slowly and is retained. Temperature inversions are the result. Shortly after dark, when the west surface of a hummock may have cooled to 35° C or so, burning hot sand of 50° C may be found an inch or two below the surface (Figs. 9, 10). This fact may be correlated with the anomalous emergence habits of some nocturnal snakes and lizards, which might not be able to reach the surface until this barrier of heated sand has dissipated.

Deeper below the surface, sand temperatures become more uniform through the day. At depths of two feet or more the change is almost completely a seasonal one. Seasonal inversions occur. The temperature of deep sand layers gradually builds up during the summer and when winter temperatures have cooled the surface sand, warmer layers underlie it. (See Cowles 1941 and Smith 1932.)

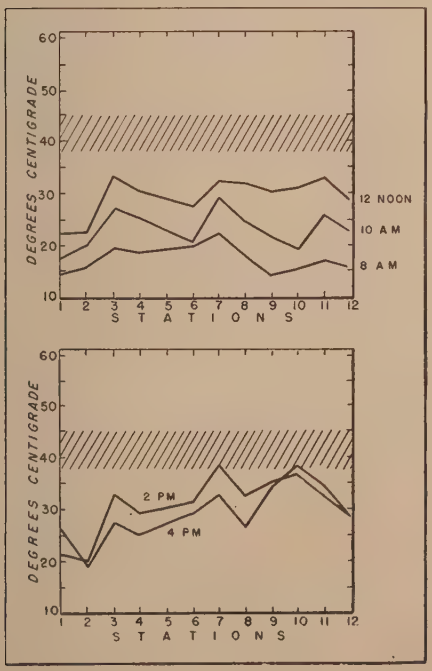

Fig. 9. Sub-surface temperatures, March 12, 1948. All temperatures are below or within the optimum activity temperature range of *Dipsosaurus*. In comparison with surface temperatures taken contemporaneously, subsurface peak temperatures lag behind and inversions between the dune surface and subsurface layers are the result.

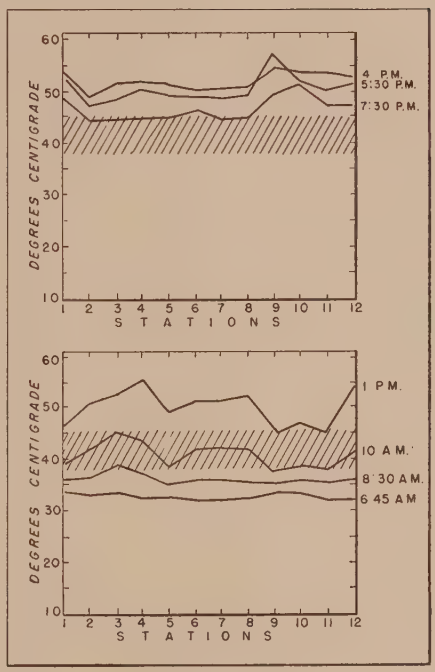

Fig. 10. Sub-surface temperatures, July 12, 1948. Afternoon temperatures at all stations exceed the tolerance range of *Dipsosaurus*, this situation obtaining until after sunset. Daily retreat must occur at deeper levels. Emergence of nocturnal reptiles may be controlled by the temperature of this heated subsurface layer.

In this area of uniform sand hummocks the correlation of the activities of *Dipsosaurus* with these temperature relations is surprisingly great. For example let us consider the daily activities of a single desert iguana during the summer months. First, the cue which brings the lizard out of its burrow in the morning is unknown. Emergence of many lizards seems to be initiated by light. *Dipsosaurus* may often live in a burrow with a plugged entrance, thus in dark-

ness, day or night. Both the roof and entrance plug seem always too thick to allow light penetration. Miller (1944, p. 285) indicates that light penetrates sand from 3 to 5 millimeters. The factor here is most probably heat, which might well be effective through the inch or two of sand blocking the entrance. *Dipsosaurus* has never been seen abroad with the first rays of the sun but is the last of the lizards to emerge. In fact, emergence is so late that the activity periods of *Uma*, the fringe-footed lizard, and *Dipsosaurus* overlap for a very short period in midsummer, *Uma* retreating shortly after *Dipsosaurus* emerges. These facts lend support to the idea that heat is the controlling factor in the emergence of *Dipsosaurus*. Caged animals can be brought out of their plugged burrows by the application of an infra-red lamp over the entrance (see *Burrows*). Emergence itself usually consists of the lizard crawling partway out of its burrow and stopping to absorb heat. This behavior offers protection to the lethargic animal. Once the lower part of the activity temperature range is reached the animal often moves to the lee crest of a sand hummock and suns itself, maintaining extreme vigilance from this vantage point. The temperature range of animals found in this phase of the daily cycle is approximately 38°–42° C. Somewhat later in the morning foraging begins. The onset of this activity is often very striking. By driving along roads through sandy areas during this time many *Dipsosaurus* can be seen running across the road or climbing up into low bushes of *Dicoria canescens*. This plant forms the principal summer and fall food of the desert iguana over most of the Colorado and Mojave Deserts. Cloacal temperatures of the foraging animals range from 41° C to 43.8° C.

As the heat of the day begins to increase foraging ceases rather abruptly; the lizards retreat to the large creosote bushes. Many of the lizards begin to climb these bushes into the cooler upper layers of air. Cowles (1946) in his original report of this activity of *Dipsosaurus* states: "Within three-quarters of an hour more than a dozen lizards were observed at heights ranging from a few inches to 5 feet 6 inches above the ground, all of them apparently engaged in feeding on the yellow flowers, [*Larrea divaricata*] or merely resting in the shade and partial sunshine." It should be noted here that the arboreal habit continues into the summer when there are no blossoms on the creosote bushes. Cowles also reports that these arboreal sorties of the desert iguana occur just prior to the disappearance of the lizard into burrows. Cloacal temperatures of animals taken from the branches of bushes range from 41.0° C to 44.8° C. While aloft the lizards are no longer in the heated surface layers of air but are usually wholly or partly exposed to the sun. Reflectance is usually at a maximum; the lizards are blanched by melanophore concentration. *Dipsosaurus* is quite wary at this time.

Following this arboreal stage of the daily summer cycle the lizards seek shade in the coolest portions of the hummock. During the summer, temperatures near the upper limit of tolerance may occur over the entire dune by 10 or 11 A.M. and just prior to this time the animals are usually found under branches on the northwest part of the hummock (stations 1, 5, 9, see Fig. 4). At this time the animals are quite quiescent and seem to rely largely upon concealment for protection. They are easily captured with a lizard noose. In general, cloacal temperatures range from 41° C to 45° C at this time. One exceptional record for an emaciated adult female was taken on July 10, 1948 at 10:15 A.M. A cloacal temperature of 46.4° C was recorded for this animal. Before the temperature was taken it was noted that the lizard was resting under a creosote bush branch, with its tail slightly raised off the sand. The tail twitched continually. The animal's mouth was not open. This animal was undergoing ecdysis and apparently had just emerged from egg-laying. The

temperature was checked with two thermometers, one of which was later recalibrated in the laboratory and found to be accurate. Once the animal was noosed and picked up the low temperature of my hand caused it to cool rapidly. Sand temperature at the point of capture was 46.8° C; air at 1 cm, 46.0° C. This record is, so far as I know, the highest voluntarily tolerated body temperature recorded for any reptile in nature.

If habitat temperatures continue to climb *Dipsosaurus* will leave the shelter of these shady spots and enter burrows. The fact that these animals have been noted to leave their sheltering bush and race across open sand directly to a hidden burrow indicates that burrows are not used at random but that a definite burrow forms the home of one or more animals. Also this fact points to the probability that the desert iguana will stop in the course of its feeding forays and seek shade in any available bush when temperatures become intolerable.

Temperatures have been taken in burrows dug by *Dipsosaurus*. During the heat of the day air and sand temperatures ranged from 35° C to 38° C in the bottoms of these burrows (July).

Dipsosaurus remains in these open burrows during midday and may make short forays near the entrance occasionally. If late afternoon temperatures are moderate enough a second, more restricted period of activity may occur. The sequence of events outlined above is rather general, with each phase overlapping the adjacent phases in variable degree, even in the markedly uniform habitat near 1000 Palms Junction. In other areas where the dunes and hummocks have not been regularly oriented by the wind the diurnal cycle is more obscure because of the wide variety of temperature situations available. The lizards continue to emerge and retreat in relation to their temperature tolerance thresholds. Some individuals may happen upon particularly well shaded locations and remain above ground after all others of the species have been forced below.

However, the onset of feeding periods has been observed in areas of uneven topography. Furthermore the beginning and cessation of these periods were rather sudden in all cases noted, regardless of topography. One trip down a road may reveal few active lizards and a few minutes later during the return trip lizards may be very evidently abundant, running over the road and adjacent sandy areas. Several genera of lizards show this sudden increase in activity, including *Dipsosaurus, Uma, Callisaurus* and *Phrynosoma.*

Occasionally *Dipsosaurus* has been noted on the roads after dark. On April 16, 1948, at 9:10 P.M., an adult with a cloacal temperature of 34° C was found on the 1000 Palms Junction road. Cowles (1941) states: "A recent trip during late October produced only one *Dipsosaurus,* a juvenile taken at night between 9 and 10 P.M. on the highway near Palm Springs." Klauber (1939) gives 4 instances of nocturnal activity for *Dipsosaurus;* from 9:05 P.M. to 10:50 P.M.; with air temperatures ranging from 88° F to 92° F.

The activity temperature range of *Dipsosaurus* is shown in Figure 11. No sexual difference in temperature preference was demonstrable from these data. Nor has such a difference been demonstrated for other lizard genera. Bogert (1949) states, "Differences between the sexes as far as body temperature preferences are concerned appear to be nil with regard to *Cnemidophorus tigris, C. sexlineatus, Sceloporus magister* and *S. woodi.*" The very high mean activity temperature shown (42.1° C ± .005) supports the casual observations of Klauber (1939) and Johnson *et al.* (1948) that *Dipsosaurus* remains active during hot summer days as long as or longer than other desert lizards. The relation of this natural activity range to experimentally determined lethal temperatures should prove to be of great interest as *Dipso-*

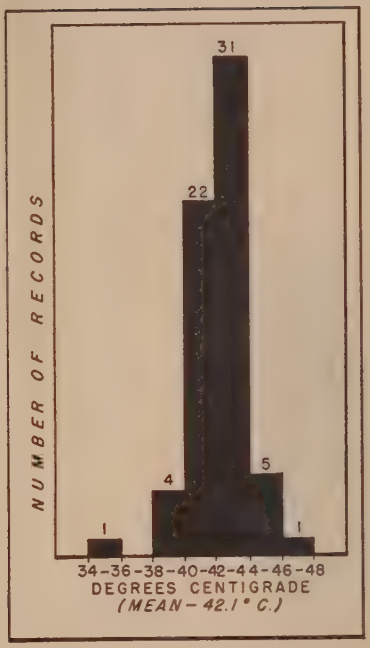

FIG. 11. Summer activity temperature range of *Dipsosaurus dorsalis*. This graph represents 64 diurnal cloacal temperature records from June, July, August and September. Mean: 42.1° C, standard deviation: .031, 2 times standard error of the mean: .005.

saurus almost certainly is active normally at body temperatures which would prove fatal if maintained for a long enough period of time (see Cowles and Bogert 1944). If such a situation exists the lizard has achieved what must be near the ultimate in behavioral adaptation to high temperatures.

Ecdysis and possibly egg-laying may have an effect upon the ability of desert iguanas to control their body temperatures. Of 7 cloacal temperature records over 44.0° C, two were of females which had just emerged from egg-laying and were undergoing shedding and two were of shedding males.

LIGHT AND COLOR

Many species of diurnal lizards have peritoneal layers that are black with melanophores (see Klauber 1939, p. 75). In *Dipsosaurus* the blackened peritoneum is present only where the membrane is attached to the body wall; elsewhere it is transparent. The mesenteries are transparent. The gall bladder and the large blood vessels of the liver are black. The pineal region of the brain is also a site of melanophore concentration. Distribution of darkened areas differs in other genera. For example, *Crotaphytus* has portions of its throat membranes blackened.

The exact function of these black layers has not been experimentally defined although it has been the center of some speculation. Klauber (*loc. cit.*) states: "The fact that some rays tend to penetrate ordinary reptile surfaces, particularly when these are light in color, may be assumed from the presence in many reptiles of a black peritoneum previously mentioned, particularly in the desert diurnal forms. . . . The color of an internal film bathed on each side with moisture can only be explained on the theory of its effect on external incident radiation. It could hardly be important from the standpoint of conserving internal heat, because of the low metabolic temperature-differential of poikilothermous animals, and the all-important part that conduction would play with respect to such heat. Rather it seems to be a second line of defense against the penetration of injurious rays, for an internal dark film cannot reduce the total thermal flux." Ginette (1942) has shown in fishes and amphibia that perivisceral and meningeal melanophores dilate after administration of post-hypophyseal extract and that they are concentrated in areas where the body walls are thinnest and where omenta are absent. It is Ginette's view that these dark layers act as a pigmentary screen against harmful radiation. Kleinholz (1938) has shown that hypophysectomy in *Anolis* results in permanent skin pallor but reference is not made to the peritoneal membranes.

Ultraviolet wave lengths have been shown to have a variety of deleterious

effects upon organisms. One of the most important of these effects is heat sensitization of living tissues. Giese and Crossman (1945) have shown that the action spectrum for sensitization to heat was similar to the absorption spectrum of unconjugated proteins such as globulins and albumins. Clark (1935) demonstrated on lens tissue (mammalian?) that ultraviolet-altered albumin will flocculate even above the low temperature of 4° C, whereas this effect is not observed in normal albumin below 40° C. Various effects of ultraviolet light have been shown upon nucleic acid and nucleoproteins. The most important of these appears to be depolymerization which may account for observed cessation of cell division and mutagenic effects. Notwithstanding the fact that visible light has been shown to reverse some of these effects (Geise 1950) it is highly probable that the blackened peritoneum is an ultraviolet screen. Very high light intensities both in the visible and ultraviolet portions of the spectrum are often encountered in desert sandy areas, and because of intense reflection from whitish sands, indigenous animals are effectively surrounded by radiation, often including their ventral surfaces. Desert lizards, such as *Dipsosaurus,* could not survive in their extreme thermal habitat if any great degree of heat sensitization were induced in them by ultraviolet radiation. Also, rapidly proliferating cells, such as are found in germ tissue, must be protected if reproduction is to be successful. These cells, with large active nuclei, are especially susceptible to ultraviolet damage.

However, the anomalous presence and absence of melanophore-darkened layers throughout the Reptilia suggest that this arrangement may be merely a function of random pigment deposition.

Atsatt (1939) has discussed the changes in coloration of *Dipsosaurus* with increased temperature and stated "In the sunshine, on a cool morning, this lizard is dark, several shades darker than the sand; in the hot midday it is as light as the sand. . . . Experimentally the light phase can be induced in the desert iguana by high temperature. The critical temperature for the light phase is high; undoubtedly this is associated with the ability of this lizard to stand much heat." Extremely warm animals (those with cloacal temperatures of 44.0° C and above) continue to blanch and finally become lighter than their background color. Therefore at both extremes of the thermal activity range of the desert iguana it is not closely matched to its substratum color.

In addition to the effects of melanophore expansion and contraction *Dipsosaurus* varies in color geographically in genetic response to varying soil colors. For example, the lizards of the Gran Desierto of northwestern Sonora, Mexico, possess a dorsal pattern of rusty brown lines and ocelli which is similar to the color of the sand upon which they live. The Coachella Valley lizards are white with a grey or blackish pattern and the sand upon which they live is white or grey. This color response is general rather than specific. Localized differences in soil color are not well correlated with similar variations in the animal's coloration. This fact may in turn reflect the considerable powers of locomotion of *Dipsosaurus* and a marked tendency to congregate in summer and fall seasons in areas of abundant food supply, thus increasing the degree of panmixia and thereby reducing the possibility of sharp, localized background color matching (unless, of course, the animals occupy the same home range, year after year, during the breeding season).

Food Habits

It is obvious that an animal subsisting largely upon green leaves and flowers, as *Dipsosaurus* does, must shift its diet through the months of activity as flowering and leafing seasons wax and wane. Because of this expected shift the stomach analysis records presented here have

been divided into three groups: spring diet (April), summer diet (June and July), and fall diet (September). Because food plants undoubtedly differ over the geographic range of the genus only animals from the Coachella Valley, Riverside County, California, were used in the food analysis. All the animals used were captured by myself or one of my field associates and none was kept alive more than a very short period after capture. None was fed.

First examination of stomach contents records shows that the lizard is not strictly herbivorous (see Table II). Important amounts of insect food are taken. The fact that insects are nearly absent from the fall diet records is probably due to the small sample examined for that season. The virtual absence of insects in the spring diet is probably not a result of sampling but a reflection of the desert iguana's strong preference for the blossoms of the creosote bush (*Larrea divaricata*). *Dipsosaurus* probably augments its diet by scavenging. The remains of *Dipsosaurus* and *Phrynosoma* found in stomach contents were quite obviously carrion. Klauber (1939, p. 84) says: "While *Dipsosaurus* is largely herbivorous it is not exclusively so. One was observed to eat ants and mealworms in captivity. On another occasion (May 12, 1929) I found a specimen with a piece of the skin of a *Uma notata* in one corner of his mouth. However this was not fresh and may have been picked up from the remains of a dead individual."

Table II. *Stomach contents of the desert iguana*

	Spring (April) No. of stomachs	Approx. % by vol. of total
Plants		
Larrea divaricata (flowers)	17	85
Animal and other		
Fecal pellets (mammal?)	12	10
Bees	2	trace
Sand and shell fragments	4	trace
Number of stomachs examined:	17	
	Summer Months (June–July)	
Plants		
Dicoria canescens (leaves)	9	45
Flower heads of composite (*Stephanomeria* ?)	3	10
Tribulus terrestris (leaves) (Puncture vine)	1	trace
Coldenia sp. (leaves and flowers)	1	5
Trifolium sp. (leaves)	3	20
Seeds	1	trace
Animal and other		
Grasshoppers	2	5
Bumble bees	1	trace
Caterpillars	2	trace
Wasps	2	trace
Remains of *Dipsosaurus dorsalis*	1	5
Remains of *Phrynosoma m'calli*	1	trace
Fecal pellets (mammal and reptile)	2	5
Sand and gravel	3	trace
Number of stomachs examined:	12	
	Fall Months (Sept.–Oct.)	
Plants		
Dicoria canescens (leaves)	6	50
Flower heads of composite (*Stephanomeria* ?)	4	25
Dalea emoryi ? (leaves)	1	10
Coldenia sp. (leaves and flowers)	1	10
Animal and other		
Wasps	1	trace
Fecal pellets	1	trace
Sand	1	trace
Number of stomachs examined:	8	

Fecal pellets occur regularly in stomach contents. These pellets are most commonly taken in the springtime when *Larrea* flowers form the great bulk of the lizards' diet. Sand and shell fragments are picked up by indiscriminate licking. Individuals have often been noted, in the laboratory and in the field, wandering along licking at various objects such as little pebbles, dried leaves, and each other. Between individuals this habit may offer some sort of specific recognition. In the fringe-footed lizard (*Uma*) the licking habit appears to be closely tied to sexual recognition (Norris, MS.).

The high percentage of creosote-bush flowers in the spring diet is interesting in view of the fact that all or nearly all northern and central populations of the desert iguana occur where the plant is common. In fact, the northern range limits of *Dipsosaurus* coincide quite closely with those of the creosote bush. *Larrea* occurs at higher altitudes than does the desert iguana and somewhat farther north in places (*e.g.*, Goldfield, Nevada) but as dwarfed plants occupying marginal habitats. As has been pointed out earlier the lizard is seemingly excluded from altitudes above 3,200 feet by climatic extremes. To the south, in Sonora, Sinaloa and Baja California, *Larrea* is often quite sparse or absent in areas

occupied by *Dipsosaurus* and other plant species must supply the spring food. The food cycle is undoubtedly much different in regions of summer rainfall. In these regions, not only are plant species much different in general from those of winter rainfall areas, but also growing and flowering seasons are shifted from spring to summer. Insects, too, are most abundant during the summer.

No parasites were found in the stomachs of *Dipsosaurus*. Even so, it seems possible that intestinal parasitism may occur in view of the amount of insect material ingested. However, host specificity of intestinal parasites may have left the lizard entirely free from infection of this sort.

Summary and Conclusions

1. *Dipsosaurus* is a genus of medium-sized iguanid lizards common over much of the Mojave, Colorado, Sonoran and Baja Californian Deserts, and along the southern fringes of the Great Basin Desert.

2. The arid subtropical scrub habitat, in which the southern part of the genus occurs, is thought to be of relatively great antiquity and to have once been much more widespread than at present. North American deserts are thought to be comparatively new geographic features. *Dipsosaurus* may occupy its northern desert habitats by virtue of a measure of preadaptation evolved in the older habitat.

3. Humidity extremes may be important in inducing aestivation and sudden summer increases in activity. Moisture may, in part, account for the death of hibernating juvenile lizards, by increasing the heat conductivity of sand overlying burrows.

4. *Dipsosaurus* is most common in sand habitats though it occurs in rocky stream beds, on bajadas, on silty flood plains and on clay soils.

5. *Dipsosaurus* occupies areas subjected to periodic transitory flooding but does not inhabit areas in which standing water covers the land for any considerable length of time.

6. Throughout the northern portions of its range *Dipsosaurus* is closely associated with the creosote bush, *Larrea divaricata*. Southern populations seem to be distributed in relation to soil types and humidity rather than plant associates.

7. *Dipsosaurus* most often occupies mammal burrows during its diurnal cycle, though at times a distinctive burrow is constructed by the desert iguana. Apparently hibernation most often occurs in burrows dug by the lizard.

8. *Dipsosaurus* exhibits home range behavior. Two and even three animals may use a single burrow at certain seasons.

9. During the breeding and egg-laying season males exhibit territorial defense. Aggressive behavior consists of a lateral display and occasional physical attack.

10. The yearly activity cycle of *Dipsosaurus* is briefly as follows: (a) Late emergence from hibernation, after all other lizard species are active; (b) Breeding during April and early May; fertilized females developing ova 1–1.2 cm in length by early June and then retreating underground for egg laying during the latter part of June and early July, whereupon they emerge; (c) Male and female pairing is observed from April through mid-July; sub-adult or incompetent adult females participating in pairs while the gravid females are laying eggs; (d) Juveniles emerge through August; (e) Adults hibernate early in the fall with juveniles retreating below ground a month or so after the adults.

11. On the desert, temperature closely regulates the activities of *Dipsosaurus* during the summer months, a predictable series of activities occurring in relation to diurnal temperature shifts within the micro-environment occupied by the genus. These thermal shifts vary in different geographic localities in relation to topography and climate.

12. *Dipsosaurus* has one of the highest normal activity ranges (mean 42.1° C ± .005) of any desert lizard. The highest voluntarily tolerated body temperature known for a North American desert reptile was recorded from an adult female, 46.4° C.

13. Certain behavioral adaptations to high surface temperatures have been noted, such as body orientation, partial burrowing, and arboreal activities.

14. Several records of nocturnal activity of the desert iguana are noted.

15. The black peritoneal membranes of *Dipsosaurus* appear to be related to the high incidence of ultraviolet radiation in its habitat. Presumably these membranes act as a shield against incident radiation, thus preventing damage to delicate tissues.

16. A limited degree of color matching to soil colors is shown within the genus.

17. Seasonal shifts in food supply have been outlined. Spring diet is composed predominantly of the flowers of the creosote bush, *Larrea divaricata.* The leaves of *Dicoria canescens,* a composite, are important in summer and fall diet. Insects and carrion form significant portions of the summer diet. Fecal pellets are regularly ingested, particularly during spring months.

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GERMINATION AND EARLY GROWTH OF GRASSES IN CONTROLLED CONDITIONS

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Widespread interest in the development and selection of both native and introduced plants for the control of soil erosion, the improvement of vegetation cover in grazing areas, and the maximum utilization of land devoted to agriculture and horticulture has focused attention on the need for basic physiological studies that relate to the survival, growth, and development of different species and races in different kinds of climate. This field of study, which of necessity embraces an appraisal and integration of genetical, physiological, and ecological factors, is so complex that to date satisfactory experimental approaches have not yet been developed. With the completion of the Earhart Laboratory at the California Institute of Technology at Pasadena, a new instrument especially useful for the resolution of such complex relationships is now available, for it makes possible for the first time critical studies on the growth of plants on a relatively large scale under known controlled external conditions (Went 1949).

The present study on the germination and early development of several species of grasses, mostly of the genus *Poa,* was conducted in the Earhart Laboratory during the summer and fall of 1950. One objective was to compare the germination and early seedling development of various species and species-hybrids at different ranges of temperature. This is of practical significance in planning reseeding programs on burned or denuded areas in arid Southern California where the establishment of young seedlings is limited to the cool winter months when rains occur. Night temperatures may then be close to freezing even at medium altitudes. Another objective was to provide background information for a broad study of physiological characteristics of importance to the establishment and survival of plants generally in different kinds of environment.

The strains of *Poa* and *Poa* hybrids used in this investigation are also being currently tested in widespread field plantings by the U. S. Soil Conservation Service, the U. S. Forest Service, and the Carnegie Institution of Washington. Certain strains of *Poa* reproduce largely by apomixis (*cf* Müntzing 1933, Åkerberg 1942, Clausen, Keck, and Hiesey 1947), and these are especially well-suited to comparative studies because the same clone can be conveniently grown from seed under different sets of controlled environments simultaneously. Moreover, data from different types of experiments, such as those from laboratory and field tests, can likewise be compared for the same genetic strain. The wide diversity of genetic strains in *Poa* includes species and races suited to a great range of contrasting climates. Data accumulated over a period of time on different clones of known genetic composition should ultimately provide basic information from which predictions on many aspects of field performance may be made with reasonable certainty on the basis of a few well-chosen laboratory experiments.

MATERIALS AND METHODS

Fourteen grasses were selected for testing. These include 5 species of *Poa,* and 5 interspecies hybrids, 1 *Bromus,* and 1

Agropyron. Two strains of some species were tested. The numbers in the list which follows are those used by the Carnegie Institution and are given here since further data on the same strains will be given in future publications by the Institution. These strains have been standardized and will be available in large quantities for range seeding and erosion control. S.C.S. indicates Soil Conservation Service numbers.

Selections were as follows:

1. *Poa ampla* Merr. (Big Bluegrass), two strains, one from Spokane, Washington, CIW 4180–12, SCS P-4914. harvested October, 1948, and one from Albion, Washington, CIW 4737–11, SCS P-4914, harvested August 18, 1949; a bunch grass producing large yields with 10 inches to 20 inches of rainfall, chiefly in the Pacific Northwest.

2. *Poa bulbosa* L. (Bulbous Bluegrass); an annual from Moscow, Idaho, reproducing vegetatively by means of bulbils. This enables it to become established very rapidly, and to adapt itself to infrequent rainfalls. It has been used as understory cover to check erosion, and as fattener for cattle.

3. *Poa compressa* L. (Canada Bluegrass) from Chorsum, Turkey, CIW 4260–1, SCS P-410–1, harvested September 8, 1945. It is sod-forming and grows on a variety of soils; widely distributed in Europe and North America.

4. *Poa pratensis* L. (Kentucky Bluegrass), two strains: one from Mather, California, CIW 4253–4, harvested August 4, 1949; one from Leevining, California, CIW 4259–3, harvested August 4, 1949. Sod-forming and summer-active, it usually prefers moderate to cool temperatures, but some strains can stand drought and high day temperatures.

5. *Poa scabrella* (Thurb.) Benth. ex Vasey (Pine Bluegrass), two strains: one from Las Posas, California, CIW 4212–1, SCS P-11040, harvested May 2, 1947 and one from Paso Robles, California, CIW 5847, SCS collection. It is a bunch grass, winter-active, found in the Coast Ranges of California.

6. *Poa ampla* (Albion) × *pratensis* ssp. *alpigena* (4683–1). *Poa pratensis* ssp. *alpigena* is considered the Northern form of *Poa pratensis;* the strain came from Lapland, where winters are long and summer temperatures of 30° C. are not uncommon.

7. *Poa ampla* × *scabrella* (Kahlotus —Las Posas, 4569–1). This hybrid and those following are described in a preliminary publication by Clausen, Keck, and Hiesey (1947).

8. *Poa scabrella* × *pratensis* (Las Posas —Mather, 4711–3), harvested Aug. 1, 1949.

9. *Poa scabrella* × *pratensis* (Las Posas —Leevining, 4559–2), harvested 1948, SCS., San Fernando Nursery.

10. *Poa scabrella* × *pratensis* (Las Posas—Leevining, 4724–4), harvested October 12, 1949.

11. *Agropyron dasystachyum* (Hook.) Scribn. (Thickspike Wheatgrass); sod-forming, tolerant of drought and poor soil. Developed by U. S. Soil Conservation Service for arid pasture land. SCS. P-1822, harvested 1949.

12. *Bromus carinatus* Hook. and Arn., similar to *Bromus rigidus* Roth (Ripgut), an annual growing on poor soils at all elevations. The strain was developed and standardized by Dr. Paul Lemmon of the U. S. Soil Conservation Service. SCS. P-11117, harvested 1949.

Selection of seed

Seeds were selected by placing them on ground glass with illumination from underneath (a photographic printing box was convenient), and picking out with forceps those which were well-filled and hard. Although well-filled seed was not always viable, while germination was obtained from some seed which was to all appearances poor, the probability of getting viable seed was increased by this method.[1]

[1] Selection of seed and preliminary studies on its viability were made by Miss Marian Popenoe.

Planting

Plastic containers $10 \times 10 \times 6$ cm. were used; gravel was placed on the bottom to a depth of 2 cm. and the dishes were filled with coarse sand. Seeds were placed in rows, 100 in each container, and covered with sand. They were then watered with a gentle spray of de-ionized water, and placed in artificial light at different temperatures as shown in Table I. Soil temperature during the germination period averaged 2° C.[2] above the air temperature during the photoperiod. The seeds were planted July 7th and the plants harvested September 24 to September 30. In addition, two groups were grown in natural daylight; one was left there for the natural day length (14 hours), with 26° day and 20° night temperature; the other was left there for 8 hours daily at 26°, then kept at 10° for 16 hours, during the first 4 hours of which it received artificial light. Subsequently, two more groups of grasses were grown in daylight, one in autumn (August 23–November 5) with an average day length of 12 hours and one in winter (October 29–January 29) in an average of 11 hours daylight. The intensity of summer sunlight varied from 4,500 to 5,000 f.c. at 9:00 A.M. and from 9,000 to 12,000 f.c. during the hours of 12:00 M. to 2:00 P.M. There was no cloudy weather.

During the autumn experiment, sunlight reached a maximum of 4,000 f.c. at noon. On cloudy days, it might be as low as 700 f.c. During the winter experiment there was less cloudy weather so that the plants received about as much light as in the autumn one.

Seeds were watered about every other day, as often as needed to maintain uniform moisture. When a seedling emerged, it was marked with a colored toothpick, the color indicating the date. It was thus possible to tell whether any had died after emergence.

After germination seemed to have ceased, containers in which little or no germination had occurred were moved to contrasting conditions and observed for further germination.

Growth in height was measured daily for the first 5 days of emergence. After 4 weeks, 6 weeks, and just before harvest at 11 weeks, the following measurements and notes were taken:

height of average plant
number of blades on average plant
width of average blade
length of longest leaf
number of blades
color
smog damage
erectness
tillering
special characteristics such as wiriness, thin stalks, etc.
general appearance of vigor

Grasses were harvested by slipping the ball of roots and sand out of the container, immersing it in water, and gently shaking it until the sand was washed out. The number of plants was counted again at this time. The plants were allowed to drain for 15 minutes on paper towels, then the tops were cut and weighed. Tops and roots were then dried at 70° C. for 48 hours, after which they were weighed separately.

A second experiment was set up, in which all seeds were germinated in one condition: day 20°–night 17°, natural daylight, in shade. The seedlings were left in this condition one month, by which time germination seemed to have ceased. They were then placed in various conditions; one group remained in the same room but was placed in sunlight.

In this experiment, the range of temperatures was the same, and somewhat similar temperature combinations were used; but the day temperature as well as the photoperiod lasted for 16 hours. Thus in the higher temperature combinations the heat tolerance of the various species was put to a more severe test. At the

[2] All temperatures indicated in this paper are in °C.

same time, certain natural conditions were simulated, in which the seed germinates in the moderate temperatures of fall or spring, and has a period of growth before the coming of hot or cold weather.

There was also, as in the first experiment, a set of conditions in which the plants were given an 8-hour day temperature and photoperiod, at day 10°–night 3.5°, day 17°–night 3.5°, and day 26°–night 10°.

In a third experiment, on germination only, seed lots were planted in soil as before, watered, kept frozen for 1 month, then placed in a moderate temperature to germinate. These were not grown further.

Three field plots were set up, at elevations of 1,000 feet, 2,500 feet, and 7,000 feet, in the San Gabriel Mountains. On the two lower plots, thermographs were set up, about 6 inches above the ground, and continuous readings taken for 3 months.[3] Minimum and maximum readings were taken nearby, at the usual distance from the ground. These two plots were watered, and were protected by screens.

Results

The most significant data of Experiment I are presented in Table I. Since the complete data cannot be shown within the space of this article, total dry weights have been chosen as a single factor which yields most of the information. In Experiment I, the growth measurements corroborated the dry weights, *i.e.*, where the weights were greater the plants were taller or had more leaves, or both, consistently throughout the test.

In Experiment II, this was not always the case, because long days at high temperatures sometimes resulted in thin-stemmed, wiry plants, or in rapid production and equally rapid death of leaves. However, the dry weights correlated well with the general vigor of the plants. Results at most critical conditions are given in Table II. Dry weights, in all of the conditions, for 6 of the grasses, are shown by curves in Figure 1.

Figure 2 illustrates the growth data for one hybrid and its parents, and for *Poa compressa,* which was selected as typical of a perennial grass with a wide temperature tolerance.

For simplicity in referring to them, temperature combinations of day 6°–night 3.5° and day 3.5°–night 3.5° are referred to as "cold" conditions; those of day 17°–night 3.5°, day 17°–night 6°, day 17°–night 10° and day 17°–night 14° as "moderate" and those of day 26°–night 6° and higher, as "hot" conditions. Day 26°–night 3.5° will be considered separately as "hot day–cold night," as it has a large diurnal difference, comparable to those occurring at times on arid mountain slopes.

Standard error was calculated for germination percentage in Experiment II, where all grasses were placed in the same conditions for the first month. It ranged from less than 1 to 4.5. There were 16 replications of each strain. Variability was high enough so that in evaluating the germination data, only the larger differences should be considered.

There was no loss of young seedlings during the period in which they all remained in the same (moderate) temperature combination. About one week before harvest, losses apparently from competition began to be suffered. Since these are hard to evaluate, the growth data are considered more significant than merely the number of plants harvested.

In the two series in Experiment I, in which day temperature was held the same —in one series at 26° and in the other one at 17°—while the night temperatures ranged from 3.5° to 14°, growth improved as night temperatures increased. That is, with a 26° day, growth was better when the night temperature was 14° than when it was 10°, and this in turn than when it was 6°, etc. (See Figure 1.) *Poa scabrella* and *Poa bulbosa* were exceptions to

[3] We are indebted to Mr. Samuel Gossard, Los Angeles County Forester and Fire Warden, for maintenance of the field plot and obtaining of temperature records at the 2,500 foot elevation.

TABLE I. *Germination and dry weight of grasses grown for 11 weeks in various combinations of temperature and light*

Species	Photoperiod..... / Light intensity.....	12 hours 750–850 f.c.											8 hours 750–850 f.c.			13 hours to 4,000 f.c.		11 hours to 4,000 f.c.		14 hours to 12,000 f.c.	
	Description.....	cold		moderate					hot day cold night	hot						autumn sunlight		winter sunlight		summer sunlight	
	Temperature Day (°C.) Night	3.5° 3.5°	6.0° 3.5°	10° 3.5°	18° 3.5°	18° 6°	18° 10°	18° 16°	26° 3.5°	26° 6°	26° 10°	26° 16°	10° 3.5°	18° 3.5°	26° 6°	20° 10°	20° 17°	20° 17°	26° 20°	20° 10°	26° 20°
Poa ampla (Spokane)	% germination/																				
	No. plants harvested	45/46	45/45	45/32	56/49	55/50	63/48	58/42	45/27	52/38	55/38	56/39	44/32	46/38	30/16	27/7	17/14	*15	*19	5/4	11/7
	G. dry wt./100 plants	no data	1.3	1.5	2.2	4.1	3.9	7.7	3.6	3.1	4.3	5.9	0.6	1.2	2.3	61.5	54.7	18.6	17.9	22.5	*63.2*
Poa ampla (Albion)	% germination/																				
	No. plants harvested	12/3	8/4	18/13	14/12	22/14	29/20	14/9	13/9	13/13	25/20	23/18	13/10	18/13	27/10	17/8	28/17	* 9	*16	1/1	6/4
	G. dry wt./100 plants	0.4	0.7	1.9	1.1	4.0	3.0	*13.2*	1.9	1.7	3.2	4.4	0.5	1.1	1.1	11.0	38.6	15.2	16.2	—	*57.3*
Poa bulbosa (Moscow, I.)	% germination/																				
	No. plants harvested	91/91	79/17	88/87	/10	87/79	83/80	64/–	76/70	73/56	78/68	60/53	98/89	99/99	91/65	36/30	27/12	*27	*18	18/18	0
	G. dry wt./100 plants	2.8	0.3	1.0	2.9	3.1	*3.2*	no data	1.2	1.9	2.1	3.0	0.6	0.5	1.7	10.7	*32.5*	9.6	10.3	2.2	0
Poa compressa (Chorsum)	% germination/																				
	No. plants harvested	40/31	51/48	50/42	44/34	61/52	44/36	48/44	44/37	53/51	47/26	46/36	49/46	48/43	49/29	37/23	37/34	* 8	*25	10/2	5/2
	G. dry wt./100 plants	0.5	0.3	0.7	0.7	1.9	2.6	*6.0*	0.8	1.2	3.0	3.3	0.3	0.4	0.7	8.8	15.0	*20.6*	15.5	12.7	11.4
Poa pratensis (Mather)	% germination/																				
	No. plants harvested	6/0	1/0	13/2	18/11	41/36	40/38	39/30	15/3	33/17	44/22	51/32	40/34	38/34	25/12	22/12	20/12	*19	*22	3/3	4/4
	G. dry wt./100 plants	0	0	1.5	0.3	1.1	1.6	*6.4*	1.0	1.0	2.2	4.0	0.7	1.9	0.2	11.7	*18.0*	6.3	8.6	0.6	3.4
Poa pratensis (Leevining)	% germination/																				
	No. plants harvested	0	19/16	46/40	43/41	81/66	73/50	72/67	6/6	37/33	84/60	82/65	75/61	80/80	25/6	no seed		*23	*18	17/17	26/23
	G. dry wt./100 plants	—	0.04	0.2	0.1	1.1	2.4	*5.1*	0.5	0.6	1.7	3.0	0.1	0.1	0.4	—	—	*12.6	*19.5*	2.0	2.4
Poa scabrella (Las Posas)	% germination/																				
	No. plants harvested	54/32	49/30	70/24	70/54	70/66	79/59	74/60	38/22	77/69	78/71	68/64	87/73	77/73	63/36	no seed		*32	*37	0	0
	G. dry wt./100 plants	0.4	0.3	0.9	0.6	1.3	1.8	*3.7*	0.7	0.6	0.8	0.8	0.5	0.4	0.3	—	—	*4.4*	3.2	0	0
Poa scabrella (Paso Robles)	% germination/																				
	No. plants harvested	26/17	27/11	61/41	71/47	24/18	42/32	67/36	16/6	64/37	69/39	48/25	49/54	50/38	70/30	38/30	28/0	*11	*16	2/2	0
	G. dry wt./100 plants	0.3	0.4	0.6	0.6	1.4	2.4	*4.6*	0.7	0.7	0.7	1.5	0.5	0.6	0.3	4.8	—	7.1	*8.9*	1.3	0

TABLE I.—(*Continued*)

Species	Photoperiod..... / Light intensity.....	12 hours 750 850 f.c.											8 hours 750–850 f.c.			13 hours to 4,000 f.c.		11 hours to 4,000 f.c.		14 hours to 12,000 f.c.	
	Description.....	cold		moderate					hot day cold night	hot						autumn sunlight		winter sunlight		summer sunlight	
	Temperature Day (°C.) Night	3.5° 3.5°	6.0° 3.5°	10° 3.5°	18° 3.5°	18° 6°	18° 10°	18° 16°	26° 3.5°	26° 6°	26° 10°	26° 16°	10° 3.5°	18° 3.5°	26° 6°	20° 10°	20° 17°	20° 17°	26° 20°	20° 10°	26° 20°
Poa ampla × *pratensis alpigena*	% germination/																				
	No. plants harvested	1/0	0	5/2	7/6	5/3	21/16	11/–	8/2	2/1	9/5	17/8	5/3	9/6	5/1	11/6	21/21	—	—	0	0
	G. dry wt./100 plants	0	0	1.2	1.1	2.5	4.3	no data	1.9	0.1	2.2	4.1	0.5	0.5	0.7	31.0	*35.9*	12.0	16.7	0	0
Poa ampla × *scabrella*	% germination/																				
	No. plants harvested	8/5	15/6	14/11	3/2	15/12	11/8	5/–	1/0	10/6	11/8	11/6	7/3	6/4	11/6	30/13	14/–	*12	*15	0	0
	G. dry wt./100 plants	0.3	0.6	0.9	0.3	3.1	*4.1*	0	0	0.5	0.8	3.6	0.5	0.8	0.6	7.8	—	7.6	*10.1*	0	0
Poa scabrella × *pratensis* 4559–2	% germination/																				
	No. plants harvested	13/no data	2/no data	5/4	9/8	10/2	10/6	3/no data	2/1	9/3	5/1	5/2	10/4	6/2	2/1	5/4	8/3	* 2	* 4	0	0
	G. dry wt./100 plants	0	0	0.8	0.8	1.6	2.4	0	0.1	0.5	2.7	0.9	0.6	0.5	0.1	6.3	*14.3*	8.5	9.0	0	0
Poa scabrella × *pratensis* 4724–4	% germination/																				
	No. plants harvested	27/22	18/17	36/25	22/14	44/33	35/27	43/	26/14	39/34	38/12	38/30	41/41	38/38	22/12	15/9	12/8	-	—	12/2	6/0
	G. dry wt./100 plants	0.3	0.3	0.7	1.0	2.1	*4.1*	0	0.8	0.6	1.6	2.2	0.3	0.4	0.3	15.4	*31.1*	no seed		11.2	0
Agropyron dasystachyum	% germination/																				
	No. plants harvested	50/44	72/42	58/53	55/54	70/51	45/35	67/–	61/56	68/58	40/32	39/19	51/39	37/37	65/52	30/33	42/–	*24	*23	48/44	54/17
	G. dry wt./100 plants	0.4	1.5	1.1	1.8	3.8	2.1	0	1.8	2.5	4.4	*10.1*	0.8	0.9	1.1	17.2	no data	15.5	8.0	13.0	*50.3*
Bromus carinatus	% germination/																				
	No. plants harvested	55/45	80/71	62/56	64/72	61/61	77/39	68/–	63/53	61/61	31/27	57/33	67/67	70/67	64/47	42/20	35/8	*30	*28	43/37	48/11
	G. dry wt./100 plants	1.1	1.9	3.1	2.8 seed	3.9 seed	*7.2* seed	0	2.0 seed	1.6 seed	3.5 seed	6.9 seed	1.7	2.7	2.4 seed	19.9	11.5	*25.7*	25.3	5.5 seed	10.9 seed

* Figure given is number of plants harvested. These plants were all germinated in day 20°, night 17°. Italicized figures for dry weights indicate optimals.

TABLE II. *Growth of grasses germinated at day 20° C.–night 17° C., moved after 1 month to various temperature combinations. In all of these the photoperiod and the duration of the day temperature was 16 hours*

	Optimal temperature (°C.)		G. dry wt. per 100 plants at optimal	Limits of tolerance
	day	night		
Poa ampla (Spokane)	18°	3.5°	17.1	none in this experiment weak stems at day 26°–night 10°
Poa ampla (Albion)	10°	10°	12.6	hot day–cold night chlorotic at day 3.5°–night 3.5°
Poa bulbosa (Moscow, I.)	10°	10°	12.2	hot day–cold night hot conditions
Poa compressa (Chorsum)	18°	10°	14.0	none in this experiment
Poa pratensis (Mather)	18°	16°	19	hot day–cold night
Poa pratensis (Leevining)	10°	10°	9.6	hot day–cold night
Poa scabrella (Las Posas)	10°	3.5°	4.7	hot day–cold night hot conditions
Poa scabrella (Paso Robles)	18°	3.5°	12.3	hot day–cold night hot conditions; weak at 17°–17°
Poa ampla × *pratensis* ssp. *alpigena*	18°	16°	25.0	none in this experiment
Poa ampla × *scabrella*	10°	10°	8.3	hot day–cold night poor at day 26°–night 17°
Poa scabrella × *pratensis* 4559–2	18°	3.5°	8.4	hot day–cold night hot conditions
Agropyron dasystachyum	10°	10°	12.1	hot day–cold night hottest condition (26°–17°)
Bromus carinatus	10°	3.5°	26.6	none made seed in 3 mos. in all conditions but the coldest

this rule at the 26° day–17° night where the growth, considering color and number of blades as well as dry weight, was not as good as with a slightly cooler night. These species in general, responded better to the lower temperatures.

All the grasses germinated and grew well in the moderate conditions. Difficult conditions were the summer sunlight with 26° day, the hot conditions in Experiment II, where the day temperature lasted 16 hours; the cold conditions; and day 26°–night 3.5°. *Poa ampla, Poa compressa, Bromus carinatus,* and *Agropyron dasystachyum* were able to germinate and survive at least fairly well in all conditions. Others failed in either the hottest or in the coldest conditions. No others except *Poa pratensis* could germinate in summer sunlight, day 26°–night 20°, and *Poa pratensis* could not germinate in the cold. Some of the grasses, such as *Poa scabrella* and *Poa bulbosa,* were very successful in the cold but much less so in the hot conditions. One of the *Poa scabrella* × *pratensis* hybrids seemed to have the combined tolerances of both parents.

In Figure 2, it will be seen that *Poa pratensis* did not germinate well in the cold, but made a good stand in the hottest condition. Of *Poa scabrella*, the reverse was true. The *Poa scabrella* × *pratensis* hybrid No. 4724-4 germinated in the cold as well as its *P. scabrella* parent, and was as vigorous in the hot conditions as its *P. pratensis* parent.

In general, grasses which germinated well in a given condition also made good growth there as shown both by dry weight per 100 plants, and by general appearance. The outstanding exception was the excellent growth in summer sunlight, of all plants which germinated there, although relatively few were able to do so.

This condition seemed to destroy the viability of the seed; for when dishes in which little or no seed had germinated were placed in hotter or colder conditions than they had been in originally, some further germination resulted in all cases except that of the day 26°–night 20°, summer sunlight; in these no further germination ever occurred. In autumn sunlight at day 20°–night 17°, germination was in most cases poorer than in corresponding temperatures with artificial light. Three of the hybrids were exceptions to this.

In Experiment II, in which plants germinated in a moderate temperature condition were moved to both hotter and colder combinations, there was in all cases better growth in the colder combinations. Optimal growth was attained at lower temperatures than in Experiment I, with the exception of *Poa pratensis* (Mather) and a hybrid, *Poa ampla* × *pratensis alpigena*. These both attained optimal growth at day 18°–night 16°, in artificial light. *Bromus, Agropyron,* and the other heat-tolerant grasses stand heat better when light intensity is high, *Poa pratensis* when light intensity is low.

In only 2 species was growth as good in the 8-hour photoperiod as in the 12- or 16-hour one at the same temperature. These were *Poa pratensis* at day 17°–night 3.5°, and *Bromus carinatus* at day 17°–night 3.5° and day 26°–night 10°. For the others, light duration was limiting. They suffered less from this limitation in the cooler temperature combinations than in the warmer one, especially as shown by weak stems and poor color.

Natural light gave far higher yields for *Agropyron, Bromus, Poa ampla,* and *Poa bulbosa.* This was in the order of 10 times as much in Experiment I. For all the grasses, natural light gave somewhat higher yields in Experiment I. But in Experiment II, *Poa scabrella, Poa pratensis* (Mather strain only), and *Poa ampla* × *pratensis* gave higher yields in artificial light.

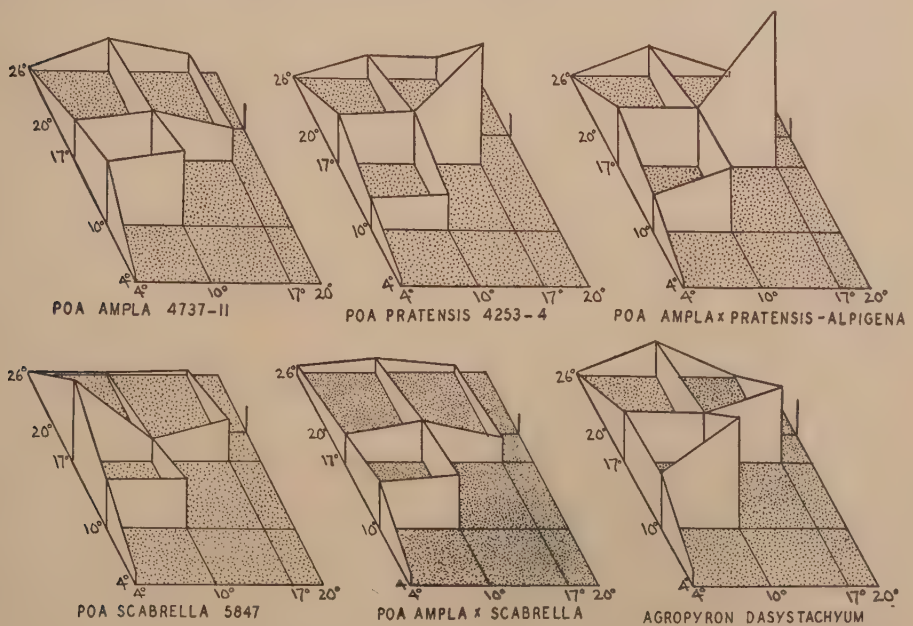

FIG. 1. Effect of various temperature combinations on dry weight of grass species and interspecies hybrids. Vertical axes represent grams dry weight. Horizontal axis represents night temperature; diagonal represents day temperature.

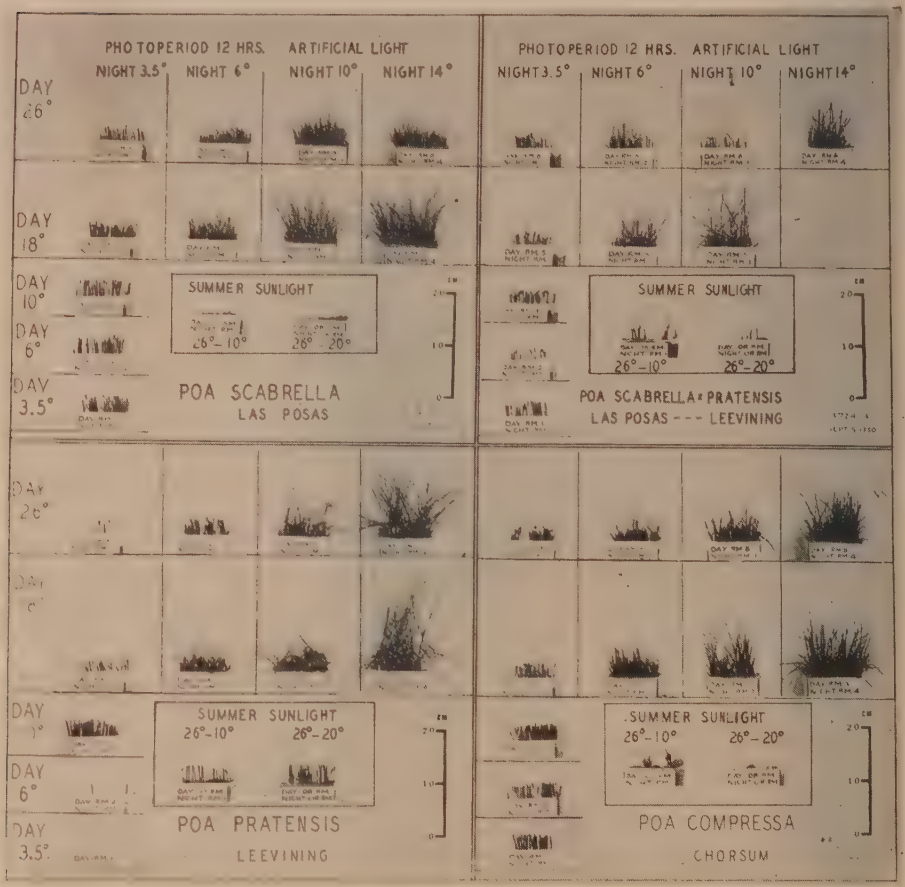

FIG. 2. Stands of a *Poa* hybrid and its parents and *Poa compressa* (Chorsum) after approximately 10 weeks from date of planting. There were 100 seeds in each container. Seedlings too small to be visible are marked with toothpicks.

The description of the responses of individual grasses which follows refers only to the strains listed, not to the species in general, since these are known to be highly complex taxonomic entities.

Poa ampla (Spokane) showed the widest temperature tolerance. It had two optimal conditions: summer sunlight at day 26°–night 20° and autumn sunlight at day 20°–night 17°. Long light duration seems to be required for best growth.

The Albion strain was similar in its responses but slightly less heat tolerant.

Poa compressa, Agropyron dasystachyum, and *Bromus carinatus* were next in temperature tolerance, with about equal range. The germination of *Poa compressa* was poor in summer sunlight at 26°–20° and 26°–10° but growth was very good.

Poa compressa grew best at high light intensity and long light duration but was not dependent upon them. It flowered early at moderate temperatures in artificial light.

Agropyron dasystachyum made a big response to summer sunlight with hot days and nights. With a cold night (10°), but the same conditions otherwise, growth was not nearly so vigorous. In winter sun-

light, plants were weak-stemmed, the blades limp, at both hot and moderate temperatures. However, cold nights, though not conducive to optimal growth, were never harmful to good establishment.

Bromus carinatus did not grow better, on the whole, in natural light than in artificial, and was better in winter sunlight than in summer. Also, in two cases, it produced better growth in the 8-hour light duration. However, it did not flower there, as it did in 16-hour light at the same temperatures, but at day 26°–night 6° it did flower in the 8-hour day. The species was remarkable for producing seed not only in many conditions but in conditions which were far from optimal for growth. The largest amount of seed was produced in conditions favorable to vegetative growth, but in the less favorable ones it flowered earlier. The effect of cold nights with hot days was to produce early flowering on weak stems. It lived out its whole life cycle in the two months, in most conditions. Therefore, it is not comparable to the other grasses, which were all perennials and consequently only in their early stages of growth. *Poa bulbosa,* although an annual, has perennial tendencies and was clearly not as far advanced as the *Bromus.* It was relatively sensitive to smog.

Next in range of temperature tolerance came *Poa bulbosa,* with a preference for the cold. The bulbils started up very quickly, 98% sprouting in 3 days, in one instance. In summer sunlight with a hot day and night (26°–20°), no bulbils sprouted. With a 26° day and 10° night, they sprouted and became established.

Poa pratensis and *Poa scabrella* had narrower temperature ranges, which overlapped. With *Poa pratensis,* germination and growth were both favored by the warmer conditions. With *Poa scabrella,* germination was good in the warm conditions as well as in the cold, but growth was definitely favored by the cooler ranges.

Both heat and cold tolerance of *Poa pratensis* were increased by germination at moderate temperatures or a pregermination treatment there. This species germinated over a long period of time, beginning very soon and continuing for more than a month. In Experiment I, none germinated in the cold conditions. In Experiment II, seed which had been kept watered and in moderate temperature for one month and had not germinated, subsequently germinated in the cold conditions; establishment was then satisfactory. The Mather strain of *Poa pratensis* flowered in artificial light, moderate temperatures, Experiment II.

Both strains of *Poa scabrella* had a wide temperature tolerance as to germination, which was good both in cold and in heat up to summer sunlight, but for growth they preferred the cold and the moderate conditions. Their optimal was in winter sunlight. They were susceptable to smog damage.

Poa scabrella × *pratensis* (4724–4) had a wider temperature tolerance than either parent, possibly as wide as both together. Since only a small quantity of the seed of this hybrid was available at the time, it could not be tested to the full extent. In size and weight, it was nearer *Poa pratensis,* the larger of the two. At its optimal, it was larger than either parent. *Poa scabrella* × *pratensis* (4559–2) was cold tolerant. Its optimal in Experiment II, at day 17°–night 3.5°, was remarkable for its low night temperature. Cold nights seemed to have no deterrent effect on growth.

Poa ampla × *pratensis* ssp. *alpigena* showed a germination percentage which was rather low. In this hybrid as in its *Poa pratensis* parent, some seedlings germinated in the cold, provided they had been kept in moderate temperatures first. Although the dry weights do not show remarkable heat tolerance, the plants which became established in the hot conditions were outstanding among other species for their deep green color and satiny, glossy texture, qualities which tended to disappear with heat in the other grasses.

The hybrid *Poa ampla* × *scabrella* also

seems to have wider temperature tolerances than either parent. It is definitely more heat tolerant than *Poa scabrella,* almost as much so as *Poa ampla,* and is considerably larger. The cold tolerance is probably better than that of *Poa ampla.*

Frozen seed all germinated when placed in moderate temperatures, except that of *Poa pratensis.* Germination of the *Poa* species was more rapid than in the other tests at these temperatures.

In the field plot at the 1,000 foot elevation, plantings made in November encountered first, a three-day rain with moderate day and night temperatures, then a heat wave in which air temperatures near the ground remained between 38° and 40° C. (102°–104° F.) for about two hours a day. Temperatures fell to 4° C. (39.2° F.) for about 4 hours nightly. This weather moderated after a week. During the ensuing two months day temperatures were usually as high as 26° C. (78.8° F.), for four hours, night temperatures as low as 2° C. (35.6° F.), for four hours. Light intensity was about twice that in the Earhart Laboratory.

Bromus and *Agropyron* germinated less rapidly than under controlled conditions but did so during the heat wave. They were stunted in growth. *Bromus* reached a height of about 12 cm. and made seed. The *Poa* species and hybrids did not germinate for about a month, and after two months measured 1 or 2 cm. in height. All strains survived, however. By spring they were still shorter than in any condition in the laboratory but their roots were from 2 to 5 times as long as their tops, and tillering was more advanced. *Poa bulbosa* flowered. *Poa scabrella* died out in the following summer.

At the 2,500 foot elevation, temperatures were moderate. The average during the first two months was day 19°–night 6° (66°–43° F.), and this was the prevailing combination. Heat sum obtained by adding hourly temperatures for 24 hours was about 300 degree-hours on many days typical of the period. Maximum and minima could still be called moderate.

All grasses germinated well and made good early growth except the *Poa scabrella* × *pratensis* hybrid 4559–2, which had a rather low germination percentage in the laboratory. *Poa ampla* × *pratensis* ssp. *alpigena* was outstanding in height and vigor. *Poa pratensis* was of a light gray-green color.

At the 7,000 foot elevation, growth is, of course, only possible after the melting of the snow. As soon as the plots could be observed, *Bromus* and some kinds of *Poa* had germinated. They looked vigorous and some had formed rhizomes. Because high winds and perhaps washing of soil had disarranged the rows, it was impossible to identify the various species of *Poa* by their position. To date, the plants though strong have not flowered, so identification cannot as yet be made. *Bromus carinatus* made a seed crop the following spring. The plants were small. *Agropyron* was not planted at this elevation.

Discussion

The adjustment of day to night temperature was always important, rather than simply the heat sum. Although in these experiments temperature and light conditions were varied so as to make comparisons with field conditions possible, water and nutrients were never limiting. This partially accounts for the rapid germination and sometimes early maturation of plants, such as the flowering of *Poa pratensis* and the seed production of *Bromus carinatus,* within two months at the optimal temperatures.

With *Bromus carinatus,* however, flowering was induced still earlier in temperatures unfavorable to vegetative growth, and resulted in production of relatively few seeds. This type of behavior may be observed in many desert annuals, such as *Bromus, rubens* L., *Pectis papposa* Gray, *Baeria chrysostoma* F. and M., *Eriophyllum wallacei* Gray, and others. They often become dwarfed and flower after only 2 or 3 leaves have developed,

even though there is still plenty of moisture in the soil, and the soil is fertile enough to produce large specimens of the same species at other times. This dwarfing is connected with such combinations of temperature and photoperiod that the plant prematurely shifts from the vegetative to the flowering stage. It is obviously of great value to the survival of the species.

It appeared that when some of the grasses were subjected to a hot day and warm night, they could make better growth, with stronger stems, if they also received a high light intensity. The grasses with the widest temperature tolerance and best able to endure the combination of hot days and cold nights were also the ones which benefited most from high light intensity.

Although the extremes of heat and cold found in nature are not reproduced in the Earhart Laboratory, the use of its hottest and coldest conditions for a suitable number of hours simulates average weather conditions rather well. A day on which the temperature rises to 35° C. (95° F.) for several hours will have a heat sum roughly equal to that of a 26° C. (78.8° F.) day of 12 hours duration. During the time of these experiments, many days occurred in which the temperature in a field plot, measured 6 inches above the ground, rose from a minimum of 7° C. (45° F.) to a maximum of 34.5° C. (94° F.). The heat sum was about 455 degree-hours which is that of the hot day-cold night combination in the laboratory when the day was 16 hours in duration.

In both the field plot at 1,000 feet where there were hot days and cold nights and in the hot day-cold night laboratory conditions, the grasses germinated rather poorly and the percentage survival was low. They were quite short and the blades, though of normal width and color, were few in number. In the plot at 2,500 feet where temperatures corresponded to the two modernate ones with the lower night temperatures (day 17°–night 3.5° and day 17°–night 6°), the grasses in both field and laboratory were of somewhat less than medium height, with a relatively high percentage germination and survival. The species which best endured difficult laboratory conditions did best in analogous ones in field plots.

Comparison could not be continued over a longer period than two months because of the change in temperatures outdoors with the advancing season. At the end of this time, plants in the field were not as far advanced in their life cycle as those in the laboratory; the annuals required 5 months to bloom even at the lowest elevation. However, it is probably significant that at 1,000 feet, the species of widest temperature tolerance in the laboratory made best growth, while the least heat-tolerant succumbed in the summer heat.

A similar parallelism between field observations and laboratory experience was found in desert annual grasses and herbaceous plants (Went 1948, 1949, and forthcoming publications). Those which germinate in winter, such as *Eriophyllum wallacei, Erodium cicutarium* L'Her. *Chorizanthe brevicornu* Torr, and *Bromus rubens,* germinate and survive best in the laboratory with nights of 3° to 10° and moderate day temperatures. Summer germinators, such as *Bouteloua aristidiodes* (H.B.K.) Griseb., *Bouteloua barbata* Lag., *Amaranthus fimbriatus* (Gray) Wats., *Pectis papposa, Portulaca oleracea* L., germinate and survive best in the high day and night temperatures in the laboratory. *Hyparrhenia hirta* (L.) Stapf., recommended for hot localities by the U. S. Soil Conservation Service, thrives only in the hot conditions in the laboratory; *Stipa cernua* Stebbins and Love, recommended for the colder ones, prefers the cold to moderate conditions. Therefore, we can conclude that laboratory tests of temperature and light requirements of plants give a good indication of how those plants will behave out-of-doors under natural growing conditions.

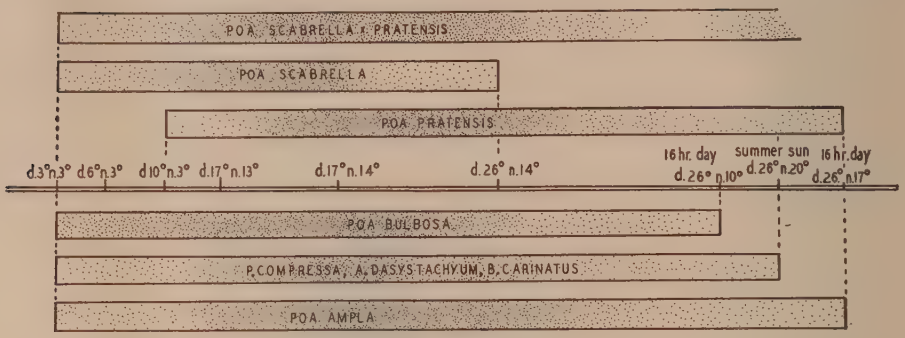

FIG. 3. Graphic representation of the range of temperature over which various grasses made satisfactory growth in these experiments. Thick stippling signifies nearness to optimal. The behavior of *Poa scabrella* × *pratensis* (4724-4) in a 16-hour day temperature was not tested, because there was only a small quantity of seed at the time.

SUMMARY

Twelve grasses were grown under different temperature and light conditions. Ranges of temperature over which they could succeed are summarized graphically in Figure 3.

An 8-hour photoperiod was limiting to growth in all grasses tested, least so to *Poa pratensis*. *Poa ampla* appeared to need a rather long photoperiod for maximum growth.

Natural daylight, having a much higher intensity than artificial light, gave yields of the order of 10 times as much for *Agropyron, Bromus, Poa ampla,* and *Poa bulbosa,* in Experiment I. Also in Experiment II, the yields were greater in natural light with the exception of *Bromus,* which had equal yields in both natural and artificial light. *Poa pratensis* and *Poa scabrella* benefited little or not at all from the higher intensity of natural light in these experiments.

Grasses in these young stages showed a preference for a fairly uniform temperature throughout the 24 hours. In general, the large diurnal temperature differences were best-tolerated by the grasses with the best endurance for both heat and cold.

Two of the hybrids seemed to combine the temperature tolerance of both parents, so that the range of temperature conditions in which they could succeed was definitely extended.

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INTERSPECIFIC COMPETITION BETWEEN TWO SPECIES OF BEAN WEEVIL[1]

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Introduction

Lotka (1934) studied mathematically the problem of the competition between two species belonging to the same ecological niche, and reached the following conclusions. When two species having the same needs or habits compete with each other in a given environment, four possible conditions of population equilibrium are deduced mathematically:

(1) Each species inhibits its own potential increase more than that of the other and both continue to exist together; (2) the first species inhibits the potential increase of the second species and drives out the second species from the given space; (3) the second species drives out the first; (4) the inhibition of each species by the other is greater than its own inhibition, and it is the initial densities that determine chiefly which species could survive.

Experimental verification of the existence of these four cases was attempted by Gause (1934) in protozoan populations and by Crombie (1945, 1946) and Park (1950) in populations of several graminivorous insects. Recently, Park (1950) investigated the competition between the flour beetles, *Tribolium castaneum* and *Tribolium confusum,* and obtained an interesting result; in one case *T. castaneum* drives out *T. confusum* and in another case the result is vice versa. He believed that this incompatibility is caused by the disturbance resulting from the infection with the protozoan parasite, *Adelina tribolii.*

The present investigation is planned with a similar purpose: to verify the interspecific competition, using two species of bean weevil, the azuki bean weevil *Callosobruchus chinensis* and the southern cowpea weevil *C. quadrimaculatus.* In addition, an examination is made of the influence of parasitization upon the outcome of competition between species belonging to the same ecological niche. The parasite used is the pteromalid wasp *Neocatolaccus mamezophagus,* which prefers both of these bean weevils as hosts without distinguishing between them.

Here, the writer wishes to express his hearty thanks to Dr. C. Harukawa for the invaluable advice given him. His thanks are also due to Miss H. Kakemi for her patient and faithful work in making the monotonous counts.

Materials and Methods

Two species of the bean weevil, the azuki bean weevil *Callosobruchus chinensis* and the southern cowpea weevil *Callosobruchus quadrimaculatus,* were used for the experiments. Both species had been reared continuously under constant conditions in the laboratory for several years.

The experiments were carried out under constant environmental conditions. In a dark incubator electrically regulated at a constant temperature of about 30° C, petri dishes about 8.5 cm in diameter and 1.8 cm in height were set. Atmospheric moisture in the dish was regulated at a constant relative humidity of about 75 per cent by means of a supersaturated solution of sodium chloride. The variety *Dainagon* of the azuki bean was used for the food of weevils. The water content of the bean was almost 15.0 per cent.

The technique used was almost iden-

[1] Contributions from the Entomological Laboratory, Kyoto University, No. 212.

tical with that described in a previous work on experimental populations of the azuki bean weevil (Utida 1941). Here, only its outline will be described. Four pairs of newly emerged weevils of both species were put in the dish prepared. Counts of the populations of both species took place at one week intervals, dead and living individuals, both female and male, being identified separately. Living individuals were lightly narcotised with ether, counted and put back in the dish. Ten-gram lots of beans were supplied as food, and were renewed every 3 weeks, a period which corresponds closely to the average time required by the weevils for completion of a generation. At each renewal of the food the remnants of food were taken away from the dish.

Method of calculating density

The number of individuals emerging between two successive counts can be obtained by a simple calculation using the number of living individuals and that of dead individuals in the two consecutive counts. The total number of adult weevils emerging in each generation can be obtained by summing up the number of emerging weevils in 3 consecutive counts, for both species of weevil require about 3 weeks for the completion of a generation. In this way, the change of population density which is caused by emergence and death of adult weevils belonging to a single generation can be smoothed out, and the resulting figures give the changes of density from generation to generation in the populations of both species.

TABLE I. *Trend of population of* Callosobruchus quadrimaculatus, *as represented by the number of emerged individuals in each generation*

Number of generation	Population A		Population B	
	♂	♀	♂	♀
1	8	8	8	8
2	104	63	63	87
3	166	148	245	133
4	143	102	135	94
5	171	125	155	95
6	63	92	103	91
7	166	122	160	132
8	168	128	134	142
9	154	140	148	111

Single-Species Equilibria

To understand the behavior of the mixed and competing populations, we must observe in advance the trend of population growth and the level of the equilibrium state in each single-species population. Experiments yielding this information for the azuki bean weevil have been conducted previously under conditions similar to those of the present experiment and have been discussed in detail (Utida 1941). The steady density of the equilibrium state in the population of the azuki bean weevil was about 400; in one population it was 390.5 and in another it was 418.9.

The trend of growth and the steady state of the equilibrium in the population of *C. quadrimaculatus* are given in Table I and represented graphically in Figure 1. Two identical populations start with 8 pairs of weevils. In the second generation the population density increases to about 150. In the third generation it reaches about 300. Thereafter, the density of population fluctuates around the mean density of the equilibrium state,

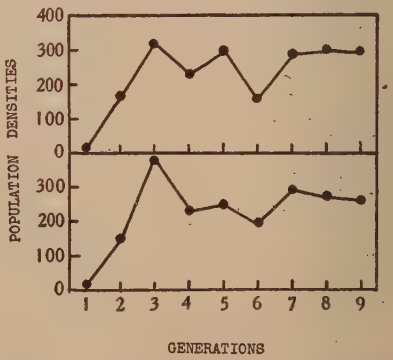

FIG. 1. Trend of population of *C. quadrimaculatus*, as represented by the population densities in each successive generation.

TABLE II. *Trend of the population when* Callosobruchus chinensis *and* C. quadrimaculatus *compete with each other*

It is represented by the number of emerged individuals in each generation.

Number of generation	Population C				Population D			
	C. chinensis		*C. quadrimaculatus*		*C. chinensis*		*C. quadrimaculatus*	
	♂	♀	♂	♀	♂	♀	♂	♀
1	4	4	4	4	4	4	4	4
2	49	56	21	36	62	66	38	30
3	35	41	142	98	69	76	138	101
4	2	7	51	53	7	3	44	52
5	0	0	212	112	0	1	193	135
6	0	0	162	103	0	0	127	160
7	0	0	172	134	0	0	133	111
8	0	0	122	128	0	0	130	104
9	0	0	104	93	0	0	110	114

which is about 250 in both populations.

Comparing the level of the equilibrium state and the trend of population growth in the two species of weevil, the following points become clear. The trends of growth are similar in *Callosobruchus chinensis* and *C. quadrimaculatus,* but the *C. chinensis* population grows slightly more rapidly than does that of *C. quadrimaculatus,* since the second-generation densities are 258 and 287 in the former population and 170 and 150 in the latter population. The equilibrium density is higher for *C. chinensis* than for *C. quadrimaculatus.* The fluctuation in the equilibrium state is almost identical in its mode in both populations.

COMPETITION WITHOUT PARASITISM

The initial populations consisted of 4 pairs of *C. chinensis* mixed with the same number of pairs of *C. quadrimaculatus.* Two such mixed populations were run in parallel to obtain the changes of the population density when both species compete with each other under the given environmental conditions. The results are given in Table II and represented in Figure 2.

In the second generation the density of *C. chinensis* became higher than that of *C. quadrimaculatus,* but in the third generation the relative proportions were reversed. After the third generation the density of *C. chinensis* decreased sharply and in the fourth generation it fell to zero and the population of *C. chinensis* was completely extinct.

On the other hand, the population of *C. quadrimaculatus* grew rapidly and attained the equilibrium state in the third generation. *C. quadrimaculatus* drives out *C. chinensis* completely in the fourth generation, and consequently the equilibrium state composed of both species of weevils can not be established. The level of the steady state in the population of *C. quadrimaculatus* was about 250 in both of the two parallel populations. It was almost equal to the value obtained

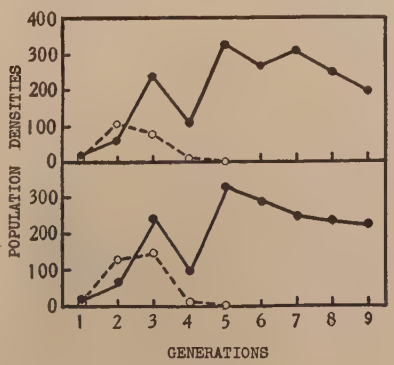

FIG. 2. Trend of population, when *C. chinensis* and *C. quadrimaculatus* compete. --○--: *C. chinensis,* —●—: *C. quadrimaculatus.*

in the homogeneous (control) population of *C. quadrimaculatus*.

Competition with Parasitism

A pteromalid wasp, *Neocatolaccus mamezophagus*, can parasitize the full-grown larva of *C. quadrimaculatus* as well as that of *C. chinensis*. When *Neocatolaccus* attacks the interacting population of two species of weevil, the relationships between the three species are very complicated.

Two populations were set up, consisting of different combinations of numbers of the host species. One population started under the dominance of *C. quadrimaculatus* and thereafter a certain definite number of the parasitic wasp was liberated in this population. Another population started under the dominance of *C. chinensis*, and thereafter a certain definite number of *Neocatolaccus* was liberated.

In both cases, the results are almost similar as represented in Table III and Figure 3. The parasite population was established and maintained relatively high density. The populations of both host species existed together and held rela-

Table III. *Competition between* C. chinensis *and* C. quadrimaculatus, *when both species are parasitized by a common parasite,* Neocatolaccus mamezophagus.

The population density of both host species is represented by the number of emerged individuals in each generation and that of the parasite is represented by the number of individuals emerged during a host generation.

Number of generation	Population E					
	C. chinensis		*C. quadrimaculatus*		*Neocatolaccus mamezophagus*	
	♂	♀	♂	♀	♂	♀
1	4	4	64	64	4	4
2	1	3	42	43	34	46
3	12	10	34	29	297	253
4	20	20	32	26	72	52
5	23	28	46	30	136	129
6	42	37	51	61	138	92
	Population F					
1	96	96	4	4	4	4
2	16	18	12	19	81	47
3	38	23	31	30	21	37
4	3	3	30	21	143	134
5	3	8	9	13	19	28
6	36	25	41	37	6	20
	Population G					
1	—	—	86	86	4	4
2	—	—	60	81	55	144
3	4	4	33	50	178	92
4	6	12	52	39	147	44
5	36	21	39	29	122	69
6	42	37	24	20	122	105

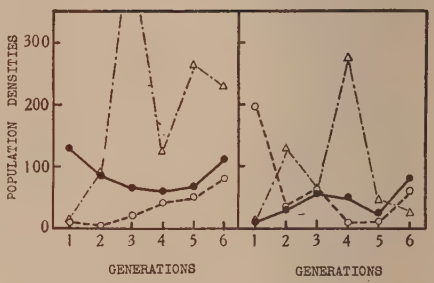

Fig. 3. Competition between *C. chinensis* and *C. quadrimaculatus*, when both species are parasitized by *Neocatolaccus mamezophagus*. Left figure: *C. quadrimaculatus* initially dominant. Right figure: *C. chinensis* initially dominant. --○--: *C. chinensis*, —●—: *C. quadrimaculatus*, —·—△—·—: *N. mamezophagus*.

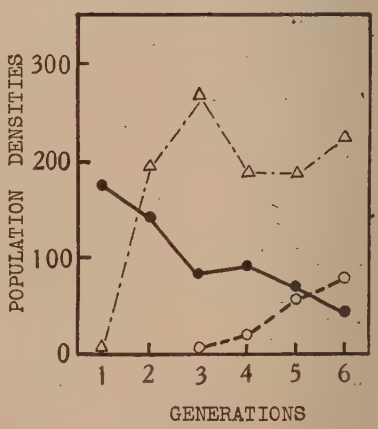

Fig. 4. Competition between two species of host and their common parasite, when *C. chinensis* is introduced after equilibrium is established between *C. quadrimaculatus* and *N. mamezophagus*. --○--:*C. chinensis*, —●—: *C. quadrimaculatus*, —·—△—·—: *N. Mamezophagus*.

tively low levels of density. Both species of weevil competed with each other, but existed together in the same universe without becoming extinct.

To confirm the present result, a further experiment was made. After the balance was established between the populations of *C. quadrimaculatus* and *N. mamezophagus,* 8 pairs of *C. chinensis* were introduced into the population. The result is given in Table III and represented graphically in Figure 4. The population of *C. chinensis* became established and existed together with the population of *C. quadrimaculatus.* The result is the same as in the former experiment, when both species of weevil were introduced at the same time with the common parasite, *Neocatolaccus.*

Discussion

The present problem has been fully investigated by Park, Crombie and others, using granary beetles such as *Tribolium, Calandra,* and *Rhizopertha,* and some mathematical postulates have been justified and important findings have been made. Although the present investigation is a preliminary one and suffers from an insufficient number of replicates compared to Park's extensive work on *Tribolium* (Park 1950), it is clear-cut in its result.

It is demonstrated that the competition between *C. chinensis* and *C. quadrimaculatus* corresponds to the second or third case of Lotka's system of competition mentioned above. It has already been shown experimentally in protozoan populations by Gause and in granary insects by Crombie that when two species with an identical niche compete with each other in a limited environment, one will drive out the other. Experimental animals used by Crombie were *Rhizopertha, Sitotroga, Tribolium,* and *Oryzaephilus,* which belong to different genera, families and even orders, while the weevils used in the present work belong to the same genus *Callosobruchus.* Competition between *Rhizopertha* and *Sitotroga* is limited in its operation to the larval stages and the mode of life of the adults of these insects is quite different, while in the present case both species of weevil compete with each other continuously all through the life cycle from the time of egg-laying to the emergence of the adult weevil. Aspects of interference include competition for oviposition site, mutual interruption of rhythmic behavior patterns by males and females, prevention of completion of copulation by individuals of the same or the other species, egg mortality caused by mechanical interference of adult individuals, and competition for food materials in the larval stage. Consequently, it is to be supposed that the process of extinction is very rapid and the end result is clear-cut, when such incompatibility obtains between species belonging to the same genus and having the same needs and habits. This conclusion seems not to hold good in the results obtained by Park on interaction between *Tribolium confusum* and *T. castaneum,* which also belong to the same genus and have entirely similar modes of life. This disagreement may be due to the fact that in the *Tribolium* populations parasitization by microorganisms, which is frequently observed, markedly influences the competition.

On the basis of this principle of interspecific competition, a theoretical interpretation was given to Motomura's formula of geometric progression in an animal community (Utida 1943). This formula, which was empirically obtained by Motomura, has proved to be of wide application. Williams' formula describing the relation between the number of species and the number of individuals in an animal population can be derived mathematically from Motomura's formula (Utida, unpublished).

As stated by Lack (1949), sympatric and allopatric speciation may be explainable by this principle of interspecific competition. In North America, the geo-

graphical distribution of the two weevils used in the present experiments is separated allopatrically into northern and southern districts.

Hutchinson (1948) pointed out two possible exceptions to this principle, (1) where external factors may act to rarefy the mixed population, so that the environmental possibilities are not completely exploited, and (2) where continual chance oscillations of the environmental variables may continually reverse the direction of competition, so that no equilibrium can be established (Allee *et al.* 1949).

Lack (1949) also claimed that two species might be able to live in the same habitat feeding on the same food without effective competition, provided that their numbers were controlled by parasites or predators. Against this is the theory of Nicholson (1933) that two species cannot persist together when both are controlled by the same predator or parasite. The claim of Lack may conform to the first term of Hutchinson's proposition, the action of parasites or predators being one of the external factors controlling the mixed population. But when mixed populations are controlled by the action of predator or parasite as an external factor, the mixed populations persist together even if the environmental capacity is almost completely utilized by the competing species. This depends upon the assumption that the parasite searches at random and parasitizes both host species without discriminating between them.

Lack's claim has not been experimentally proved as yet, except for the present experiment. When two species of bean weevil are attacked by the parasite *Neocatolaccus,* the equilibrium densities of both bean weevil populations decrease but neither species becomes completely extinct; both exist continuously, all through the experiment. This situation seems frequent and important in the host-parasite and prey-predator systems. It is likely that the mixed population of *Tribolium confusum* and *T. castaneum* parasitized by the protozoan *Adelina* provides another example. The theory of Nicholson is probably correct only when two host species compete with each other severely for the determination of their adult densities after both are attacked by a common parasite. In this case, the random searching by the parasite is not operative in regulating the equilibrium state, but Gause's general principle of competition for food between two host species is operative.

It can be concluded from the result of the present experiment that predation or parasitism plays a more important role in regulating the number of host or prey individuals than does competition between two or more species of host or prey belonging to the same ecological niche. Perhaps this conclusion may also apply when extended to the comparison between predation and intra-specific competition.

In a natural community species interact with each other as host and parasite or as predator and prey, as well as by way of interspecific competition for the same niche requirements. Neither type of interaction can be ignored, and both kinds together provide the warp and the weft of community organization. The regulatory action of inter- or intraspecific competition can be transformed or outweighed by such higher-order interspecific interactions as predation and parasitism. Accordingly it is no mistake to conclude that the abundance of a given species in nature is mainly controlled by its predators or parasites and that its competitors of the same or related species are less important than has been assumed.

Pursuing this line of reasoning, we reach the theoretical conclusion that the distinction between allopatric and sympatric species does not exist in the lower strata of community organization, but comes in only at the higher levels of carnivory. In other words, the greatest number of species (as well as individ-

uals) should be found at the lowest ecological rank in the food-chain hierarchy.

Summary

In this paper, interspecific competition was studied experimentally between species belonging to the same ecological niche. Two species of bean weevil, *Callosobruchus chinensis* and *C. quadrimaculatus,* were reared under constant laboratory conditions and counts of weevils were made every generation at regular intervals. Unispecific control populations of *C. chinensis* and *C. quadrimaculatus* grow and attain the steady state of population after two or three generations under the experimental conditions. The steady population density of *C. quadrimaculatus* maintains a higher level than that of *C. chinensis.* When both species compete within the same microcosm, the population of *C. chinensis* is depressed and falls to zero after several generations. When a paratitic wasp, *Neocatolaccus mamezophagus,* is introduced into the mixed population of competing species, the population of the wasp is established and the populations of the two weevils are reduced markedly below their level of steady state, but they exist together in the same microcosm. The same result occurs regardless of the population densities of the host species relative to each other. These results are discussed on the general background of population theory.

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CLIMATE AS A FACTOR INFLUENCING THE MASS RANGES OF WEEDS [1]

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INTRODUCTION

Weeds are considered by many individuals to be plants with such broad tolerances to environmental conditions that they are capable of invading almost any agricultural area of the globe. Although there is no denying that some weeds such as lamb's quarters (*Chenopodium album*),[3] dandelion (*Taraxacum officinale*), and many others have become almost universal in occurrence, nevertheless it can be shown that many regions have a weed flora peculiar to them. In North America, for example, the mass range or area of maximum occurrence for a weedy species may be centered in a certain floristic province such as the Great Plains and the occurrence of the plant outside this region of mass range is rather limited or sporadic.

Such areas of mass range for some weeds lead the casual investigator to conclude that some factor or factors are operating which prevent the wholesale spread of these plants. Time, of course, must be considered in all studies of plant distribution and soil factors as well as areas of cultivation and tillage practices are very important in the case of weeds. These factors, however, cannot be responsible for all distributional patterns of weeds. Climate, which is the major factor influencing the ranges of native plants, has largely been overlooked in the investigation of weed distribution. If it can be shown that climate influences the mass ranges of some weeds, it becomes a matter of considerable practical importance to study the behavior of a weed within and out of its climatic optimum. Moreover, if the spread of a weed is limited by climate, it may be possible to predict the ultimate area to be occupied by the plant.

In the investigation of mass weed range, a number of problems arise. First, since it is important that the range of a species be mapped, the question of abundance is of primary importance. Unfortunately, most herbarium specimen records give little information on the density of a weed in a particular locality. Also, when herbarium records are used entirely, false impressions of distribution may be formed since there is a tendency for botanists to collect more in the immediate vicinity of the herbarium site and also to collect plants which are rare in a locality for record purposes. To overcome these difficulties, a ground survey should be carried out where possible to supplement the data from herbarium records.

Wisconsin, on the northern edge of the Prairie Peninsula, is admirably suited to the study of the mass ranges of weeds. The state lies along the prairie-forest border, an ecotonal region or tension zone, which separates two very distinctive large plant communities, namely: the prairie to the west and south and the white pine-northern hardwood forest type to the north. Figure 1 shows the general position of the prairie-forest border

[1] Presented as a portion of a Master's thesis at the University of Wisconsin.

[2] The writer wishes to express his sincere thanks to all those who contributed to this study. He is indebted to Dr. Reid Bryson, Dept. of Meteorology, University of Wisconsin, for his many valuable suggestions in the climatic study of Wisconsin and the neighboring states. Especial thanks are expressed to Dr. John T. Curtis, Dept. of Botany, University of Wisconsin, under whom the major portion of the work was undertaken. His helpful guidance and critical review of the manuscript were greatly appreciated by the writer.

[3] Nomenclature in this paper follows Fernald (1950).

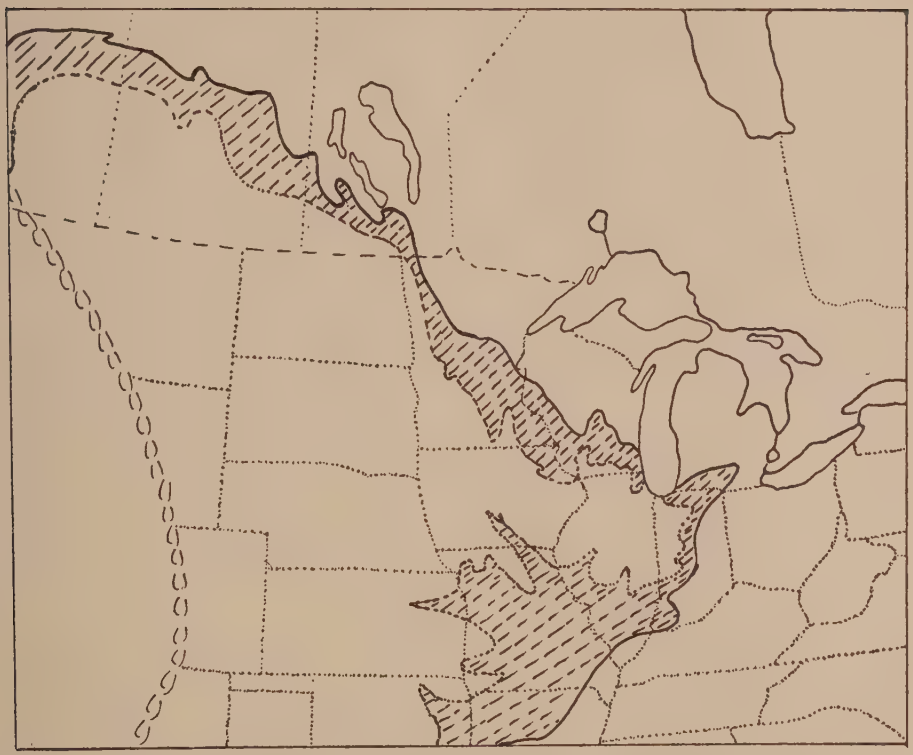

FIG. 1. The prairie-forest border tension zone of eastern North America. Stippled area is largely a savanna type of vegetation between two major communities.

tension zone extending from south-central Canada to the mid-west states. Since many of the native trees in Wisconsin reach either their northern or southern limit of range in this ecotone, it was thought that many weeds might also show similar patterns of distribution. If such paterns existed it would then be possible to obtain distributional data from adjacent states and to ascertain if climate was responsible for the over-all range of a weed in the Prairie Peninsula and along the prairie-forest border.

METHODS

A list of both introduced and native weeds was prepared in the form of a questionnaire and sent to each county agent in Wisconsin to obtain data on the abundance and habitat of each weed used in this study. This questionnaire was also sent to various agriculturalists in the Prairie Peninsula states to secure further information on weed distribution in that region. Distribution data on certain weeds along the prairie-forest border in Canada were obtained from herbarium records and weed survey reports of the Dept. of Agriculture, Central Experimental Farm, Ottawa, Canada.

It is emphasized that no attempt was made to show the complete distribution of a species. Only regions where a particular weed was present in greatest abundance were utilized. Unfortunately, the term "abundance" or plentifulness of a species is purely subjective as used in this study. Whether or not a weed is abundant in a region depends entirely on the individual making the estimate.

To overcome this subjective judgment in Wisconsin, a frequency survey by

counties was made during the summer of 1950.[4] These surveys were carried out along routes travelled from Madison in Dane County of southern Wisconsin northward to Marinette and Florence Counties in the extreme northeast, Iron and Vilas Counties in the north-central part of the state and to Burnette and Douglas Counties in northwestern Wisconsin. Different routes were followed on the northward and southward trips, thus giving a frequency survey of counties in 6 large transects radiating from Dane County in a northerly direction across the state.

The method of making this survey was as follows: first, a list of easily recognized weeds was prepared on a sheet ruled into a number of columns; then, in travelling by automobile, a frequency count was made at mile intervals in each county surveyed. Through one tenth of a mile travelled, the particular weed was checked as being present within that tenth of a mile. Then the remaining nine-tenths of a mile were traversed and a similar tenth of a mile survey made and so on, till 10 such surveys were completed, making a total of 1 mile surveyed for each 10 miles covered in each county. Only one such survey per county was made. Distances in all cases were recorded by the automobile's speedometer. Since each column on the prepared sheet represented a tenth of a mile interval, a weed could be easily checked as being present or absent. Therefore, if a weed appeared as checked off in 6 columns out of a possible 10, it would have a frequency of 60%.

This method also has some objections. First, its success depends on whether a species is in full flower and can be easily seen from a moving automobile. Second, the frequency data do not give a complete picture for any one county since they depend entirely on the area in which the survey was made in the county.

Despite some of these objections, the method shows promise of being a rapid method for making weed surveys. Since the present method was carried out more or less randomly, it yields a general picture of weed distribution over a large area in a relatively short time. Certainly, the method with modifications could be used to obtain general information which would be the basis for future intensive work. This method also records absence as well as presence, and, so far as weeds are concerned, this is a distinct advantage.

In addition to supplementing abundance data by the above method in Wisconsin, distribution was also checked as far as possible by herbarium specimens of the University of Wisconsin Herbarium and also by various persons acquainted with weed distribution in the state. Weed distribution in the Prairie Peninsula and along the prairie-forest border was checked by regional floras and weed bulletins.

Maps showing the greatest regional abundance were prepared for a number of weeds in Wisconsin, the Prairie Peninsula, and the prairie-forest border running from the Prairie Peninsula northwestward into Canada. Frequencies for each species obtained by the survey method outlined above were divided into 3 size-classes, 1 to 32%, 33 to 66%, and 67 to 100%. These frequency classes were then plotted on maps.

Climatic factors were also investigated for Wisconsin and adjacent regions as far as possible. This included the calculation of mean daily July evaporation for various stations east of the Rocky Mountains.

This was done from an evaporation formula derived by Penman (1948) in which $E = 0.376\ (VPD)\ U^{0.76}$ where E is the calculated evaporation in mm. per day, VPD [5] is the vapor pressure deficit

[4] The writer is indebted to Drs. Grant Cottam, R. P. McIntosh, and R. T. Brown and Messrs. W. E. Randall and E. E. Terrell for their assistance in the collection of field data.

[5] Vapor pressure deficit was calculated as the difference between the saturated vapor pressure for the mean July temperature and the actual vapor pressure for various weather sta-

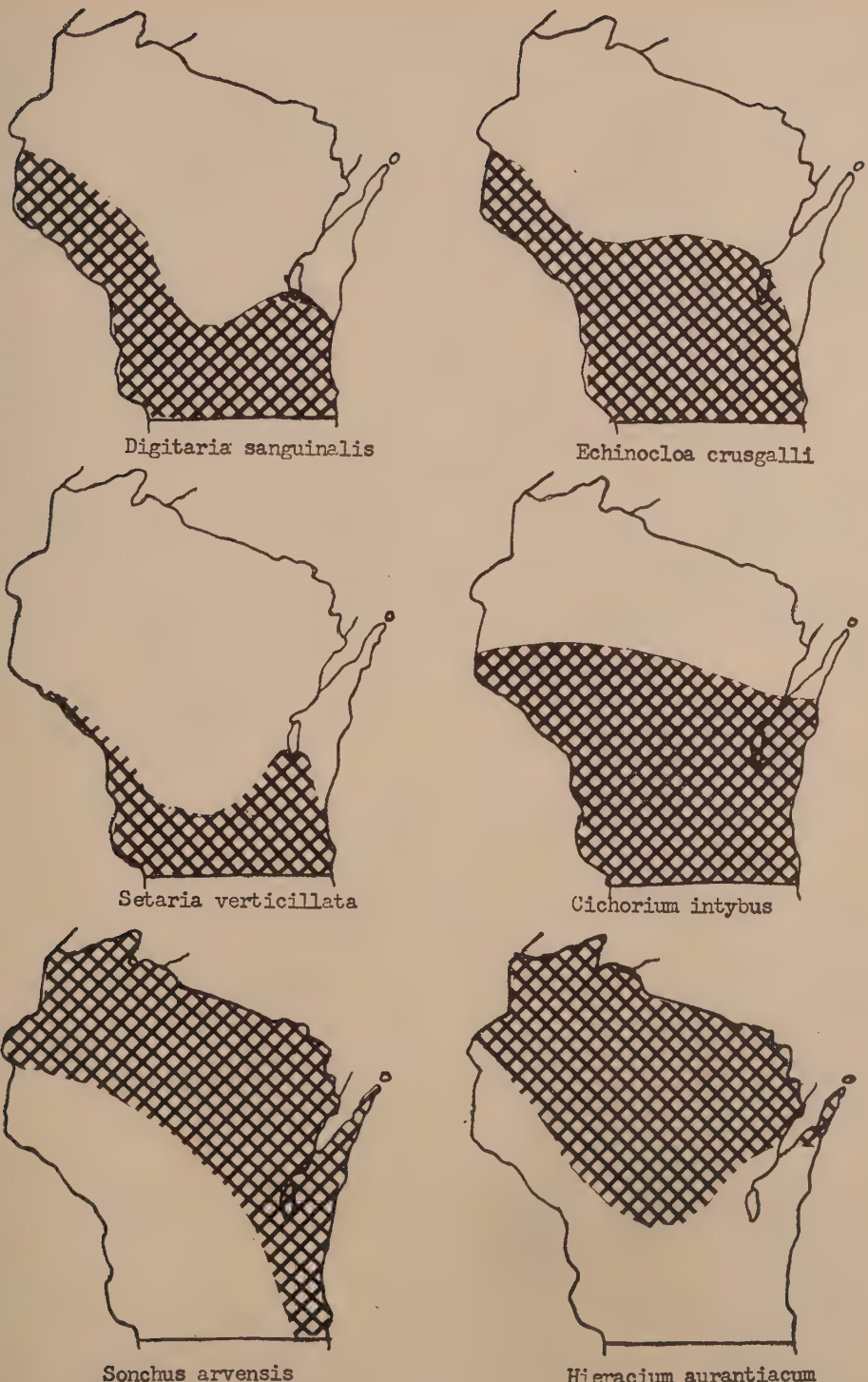

FIG. 2. Areas of maximum abundance (shown cross-hatched) for some weeds in Wisconsin.

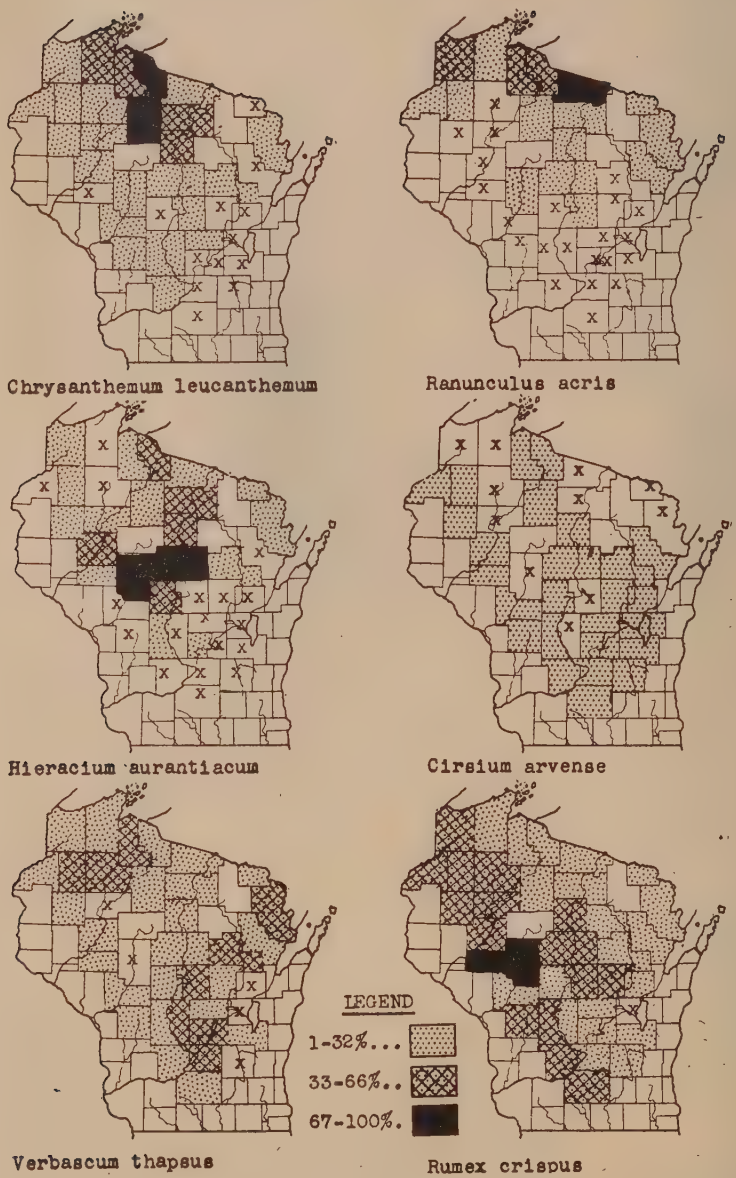

FIG. 3. Weed survey results grouped in frequency classes for six weeds in Wisconsin (counties where surveys made but weed not found are shown with an "x").

in mm. of mercury and U [6] is the surface wind velocity in miles per hour. The factor 0.376 was calculated by Penman and remains constant as long as the wind velocity is in miles per hour. If miles per day are used then this factor becomes 0.033.

Mean daily July evaporation was used since this month was considered to be a

tions calculated by A. F. Meyer in "Evaporation from Lakes and Reservoirs," Minnesota Resources Commission, St. Paul, 1942.

[6] Surface wind velocity was taken from unpublished U. S. Weather Bureau data.

good indicator of conditions of evaporation during the growing season.

Results

Weed distribution

It was found that some weeds reached their greatest abundance in either northern or southern Wisconsin. Figure 2 shows the areas of maximum abundance in the State for six important weeds. The maps were compiled from information received in the questionnaires sent to county agents and were checked by herbarium records and individuals acquainted with weed distribution in the state. The weeds included are large crab-grass (*Digitaria sanguinalis*), barnyard grass (*Echinochloa crusgalli*), bristly foxtail (*Setaria verticillata*), chicory (*Cichorium intybus*), perennial sow thistle (*Sonchus arvensis*), and orange hawkweed (*Hieracium aurantiacum*). It is seen that the mass range of the first four species is predominantly

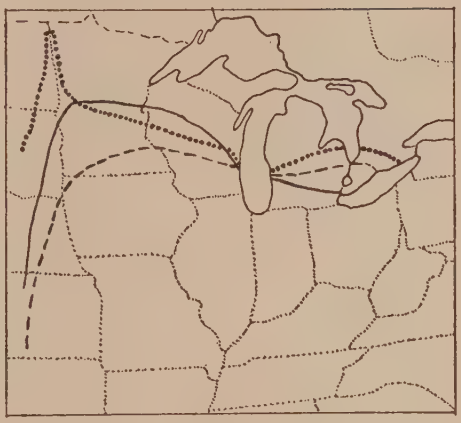

Fig. 4. Northern limit of mass ranges for hemp (solid line), velvet leaf (broken line), and great ragweed (dotted line) in the Prairie Peninsula states.

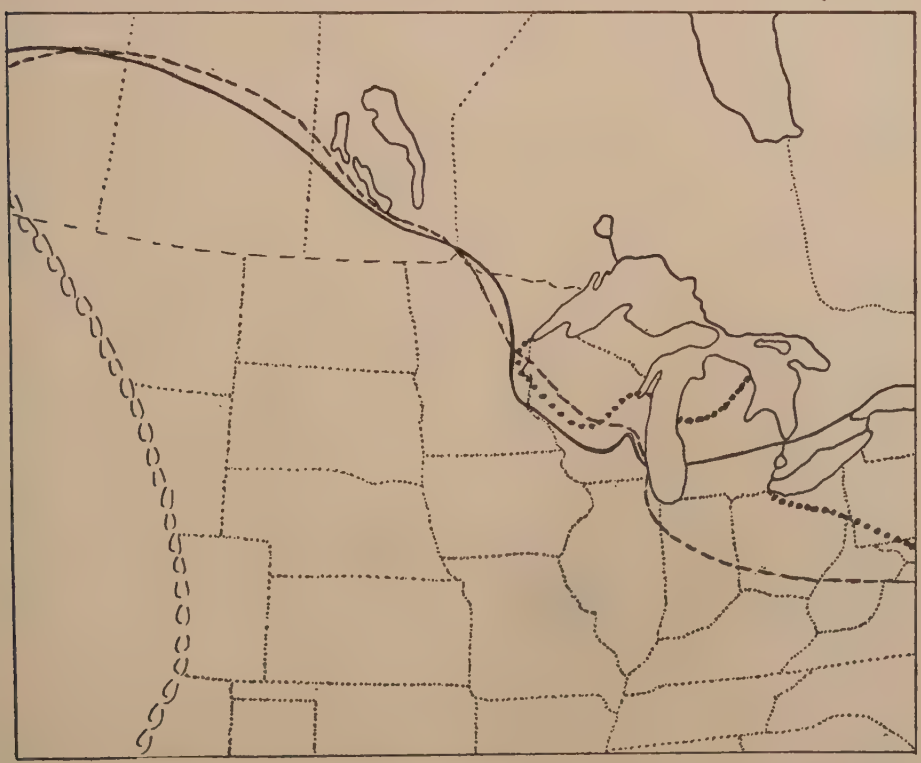

Fig. 5. Southern limit of mass ranges for buttercup (broken line), ox-eye daisy (solid line), and orange hawkweed (dotted line) along the prairie-forest border.

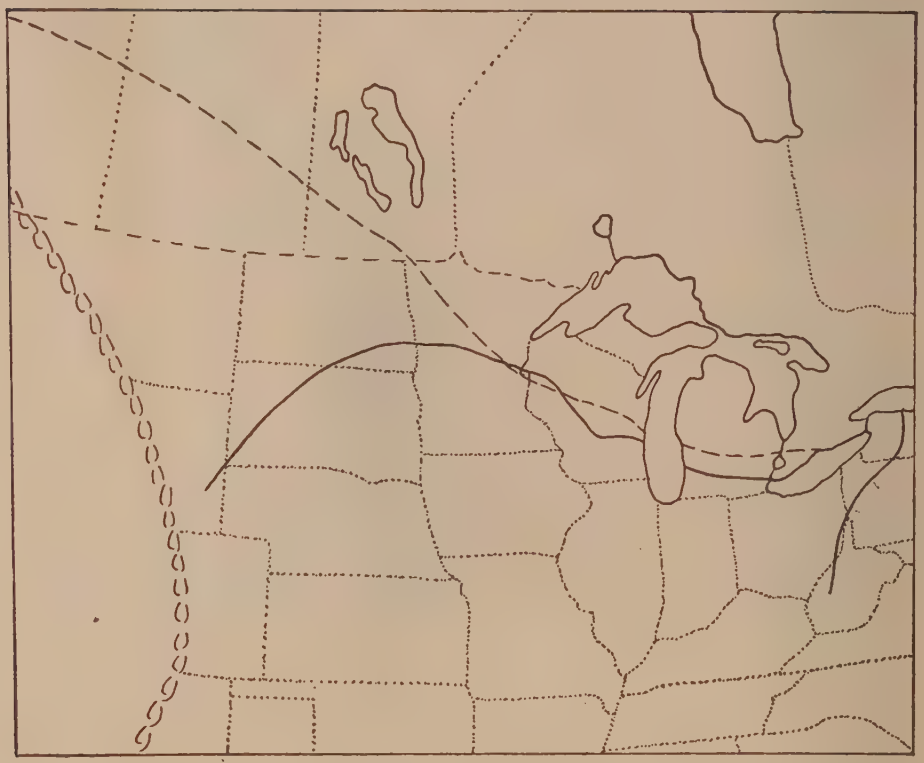

FIG. 6. Northern limit of mass ranges for buffalo bur (solid line) and goatsbeard (broken line) in the Great Plains.

southern, while the two latter weeds are northern in range.

Figure 3 shows the results of the frequency class data plotted by county for another group of weeds. Although the whole county was allotted the frequency class value based on only one survey the results show that the frequencies of buttercup (*Ranunculus acris*), ox-eye daisy (*Chrysanthemum leucanthemum* var. *pinnatifidum*), and orange hawkweed increase northward from Dane County in southern Wisconsin. For buttercup and ox-eye daisy, frequencies are greatest in the extreme northern sections of the state while the value for orange hawkweed is greatest in north-central Wisconsin. The high frequency for orange hawkweed in this region may be due to the sandy soils of the area. It is also seen that such weeds as Canada thistle (*Cirsium arvense*), mullein (*Verbascum thapsus*), and curly dock (*Rumex crispus*) show very similar frequencies both in the northern and southern sections of the state.

Figure 4 shows the approximate northern limit of mass range for hemp (*Cannabis sativa*), velvet leaf (*Abutilon theophrasti*), and great ragweed (*Ambrosia trifida*). So far as Wisconsin is concerned, it is seen that their regions of maximum abundance are similar to the "southern group" previously mentioned. The southern limits for buttercup, ox-eye daisy, and orang hawkweed are shown in Figure 5. Figure 6 shows the northern limits for buffalo bur (*Solanum rostratum*) and goatsbeard (*Tragopogon major*). The significance of these ranges will be discussed later.

On examination of all these distributional maps and comparison with the map of the prairie-forest border tension zone (see Figure 1), some rather remarkable patterns are evident. It is seen that the mass ranges of some weeds are closely influenced by factors operating in this tension zone. For example, in Wisconsin many northern weeds like buttercup, oxeye daisy, and orange hawkweed reach their southern limits in or near the same region as the southern species reach their northern limits. This region is the ecotone along the prairie-forest border.

General climate of Wisconsin

Northern and southern Wisconsin each has a distinctive climate both in summer and winter. The latter region receives a lesser amount of winter snowfall than the northern part of the state. There is a distinct rise in the snowfall gradient from less than 40 inches in the south to greater than 55 inches in the north. Visher (1945) has shown southern Wisconsin to be a region of greater freezing and thawing than northern Wisconsin where the snow cover remains until late in the spring. Southern Wisconsin also experiences more freezing rain and sleet storms than the northern part of the state.

In summer, northern Wisconsin has lower mean summer temperatures and relative humidity than southern Wisconsin. There is also a rise in the rainfall gradient going from south to north. Evaporation has been shown by Transeau (1905) and Visher (1945) to be greater in southern Wisconsin. In the matter of evaporation, Penman (1948) points out that evaporation is dependent on two conditions, namely: there must be a supply of

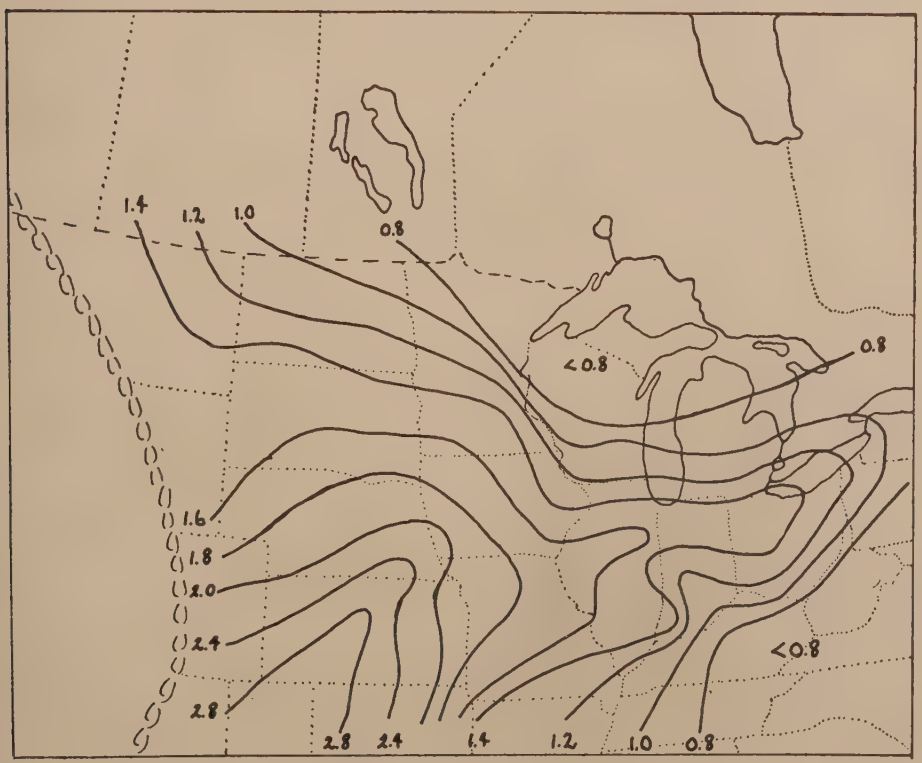

Fig. 7. Mean July evaporation in mm. per day.

energy to provide the latent heat of vaporization and, also, there must be a mechanism for removing the vapor, *i.e.* there must be a "sink" for the vapor.

Figure 7 shows the mean July evaporation in mm. per day for Wisconsin and the neighboring states calculated from Penman's formula $E = 0.376$ (VPD) $U^{0.76}$ which was mentioned earlier. Although this formula fulfills only the second condition of evaporation, the atmospheric sink, it nevertheless shows that southern Wisconsin has a higher potential evaporation than the region to the north. Checking the calculated evaporation values against observed evaporation rates, it was found that the calculated rates are not high enough to agree with the observed. Calculated values do show, however, that northern Wisconsin and adjacent regions like northern Michigan have rather uniform rates of evaporation while those in the south vary considerably, becoming higher as one proceeds into the Prairie Peninsula.

The differences in climate between northern and southern Wisconsin have been explained by Borchert (1950). He has been able to differentiate a number of climatic regions in North America east of the Rocky Mountains (see Figure 8). These are based on their position relative to the polar air streams to the north and the tropical air masses circulating into the interior of the continent from the Gulf of Mexico. Between these air streams is a large wedge-shaped region which is under the influence of dry westerly winds originating from the easterly edge of the Rocky Mountains. This wedge-shaped region is largely that occupied by the North American grassland.

Since region I is under the influence of polar air masses most of the year, it is

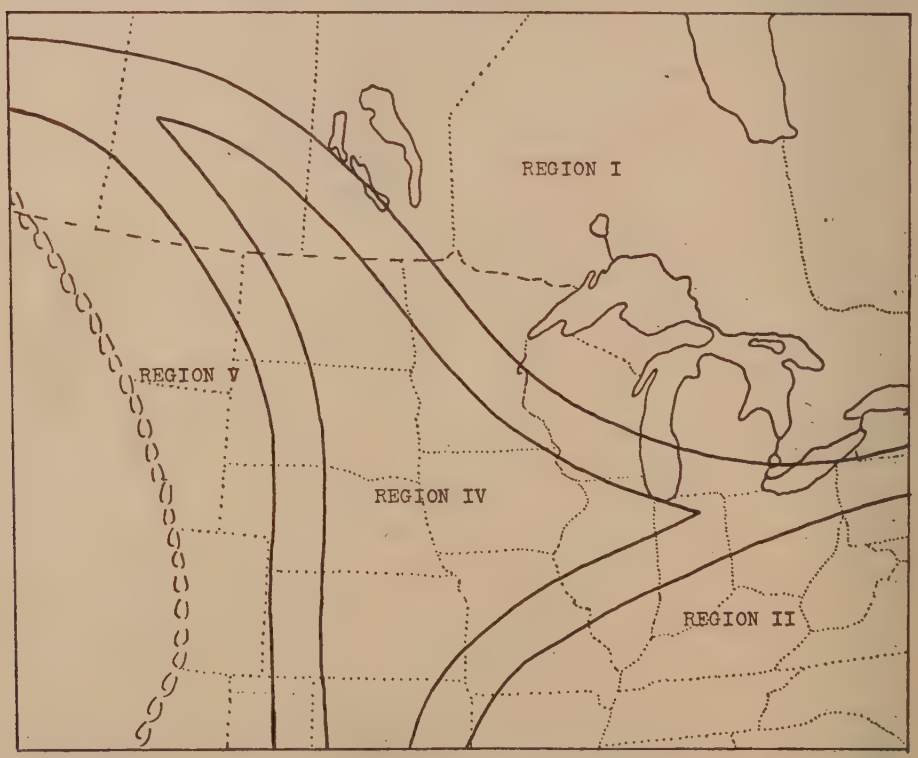

FIG. 8. Climatic regions of North America east of the Rocky Mountains (after Borchert 1950).

characterized by snowy winters and summers free from severe droughts. The climate of northern Wisconsin, then, is mostly free from wide degrees of variation both in summer and winter. The climate of southern Wisconsin falls closely into that of region IV. The winters are more like those in the Great Plains since a continental airflow in winter is characteristic of the region. Thus, southern Wisconsin in winter has frequent freezing and thawing conditions which are prevalent in the Great Plains. In summer, southern Wisconsin has a variable climate. In most years the climate is capable of supporting tree growth but occasionally droughts may occur due to the failure of the Gulf air masses to push inland. In such cases, the dry westerly flow of air enlarges the wedge-shaped region of the grassland.

It is important to note that the climate of southern Wisconsin is very different from northern Wisconsin. Since the former region lies along the northern border of the Prairie Peninsula it has a summer climate of non-uniform precipitation, temperature, humidity, or evaporation. Even winter conditions are more severe on vegetation in southern Wisconsin than to the north where plants are protected from temperature changes by an ample snow cover of long duration.

Discussion

Thus far in this study it has been shown that some weeds have areas of maximum abundance either in northern or southern Wisconsin. The limits of these mass ranges fall in the prairie-forest border tension zone which separates two distinct plant communities to the north and south. It has also been shown that the climates north and south of the tension zone are very distinctive but before any conclusions can be drawn as to whether climate is responsible for the distribution of these weeds used in this study, three important factors must be taken into consideration. These are time, soils, and areas under cultivation.

The question of time enters into all problems of plant distribution. In weed distribution in Wisconsin, it must be shown that the species used in this study have had time to migrate to their full geographic limits. Cheney and True (1892) state that ox-eye daisy was rare in Dane County in 1892. Since the plant is still rare in this county at the present time, it apparently has not increased in abundance since that date. These authors also list chicory, hemp, barnyard grass, and others as present in the county but do not list buttercup which now has a northerly distribution in the State. This weed, however, was reported by Bennett (1900) as present in Milwaukee County about 1900. This plant has not migrated to the drier regions to the west of that county. Pammel (1887) has also shown such southerly distributed weeds as velvet leaf, large crab-grass, and others to be present in abundance in LaCrosse County of southwestern Wisconsin as early as 1887. These plants are still abundant in this county but have not shown any tendencies to migrate northward. It can be concluded, then, that most if not all weeds used in this study have had time to migrate to their full geographic limits in the state.

It also may be argued that weeds found mainly in northern or southern Wisconsin may be restricted to certain great soil groups found in those regions. Thus, such weeds as ox-eye daisy, buttercup, and orange hawkweed might be confined to the podzol soils of northern Wisconsin. Ox-eye daisy, however, is found in Missouri where podzols are of very limited extent. The writer found the other two plants on Manitoulin Island in Lake Huron where they were very abundant on very shallow, calcareous soils. Moreover, velvet leaf and chicory range from the gray-brown podzolic soils of Missouri over the prairie soils of the Prairie Peninsula into southern Wisconsin.

Perhaps the main argument that can be put forth for a weed being distributed in

southern Wisconsin is that cultivated land is more limited in the northern sections of the state and, therefore, weeds found in southern Wisconsin are not able to persist farther north because they lack the necessary cultivated areas for survival. Referring back to Figure 4 showing the distribution of hemp, velvet leaf, and great ragweed, the map shows that these plants have a distinct and similar distributional pattern and that they do not tend to migrate northward in the grassland even though extensive cultivation is carried on as far north as southern Saskatchewan. Also such weeds as mullein, Canada thistle, and curly dock were shown to have similar frequencies both in northern and southern Wisconsin indicating the differences in the amount of cultivation carried on in these two regions were not important in the distribution of these weeds. It must be emphasized, however, that cultivation practices and soils may play a large part in the distribution of some weeds but, so far as the species used in this study is concerned, the role of these factors is secondary.

Turning to Figures 4, 5, and 6, it is evident that regional patterns of distribution exist for the weeds mapped. Figure 4 shows that hemp, velvet leaf, and great ragweed are very similar in mass range and that their northern limits fall in much the same region in the Prairie Peninsula. Therefore, these plants must have a close association with climatic region II shown in Figure 8. This region is one of high winter precipitation and of low evaporation stress during the summer. It is interesting to note also that some native trees have a similar range as the foregoing weeds. For example, black walnut (*Juglans nigra*) and hackberry (*Celtis occidentalis*) reach the northern border of the Prairie Peninsula which is, as previously mentioned, a tension zone. Like the weeds, these trees range into the grassland and are presumably prevented from a further western migration by the increasing aridity and high evaporation stress.

The northerly distributed weeds such as buttercup, ox-eye daisy, and orange hawkweed are adapted to climatic region I. This region is under the influence of polar air masses for most of the year yet is still a region of low plant stress. Evaporation rates are very similar to region II although mean temperatures are lower. The similarity in rates of evaporation is exemplified in ox-eye daisy which is found south of the Prairie Peninsula in abundance as well as to the north of this region. The southern distribution for this plant was not mapped owing to insufficient data. There are also native trees with ranges similar to these three weeds. Balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*), and others are boreal trees whose southern limits of distribution fall along the northern border of the Prairie Peninsula. Red maple (*Acer rubrum*), like ox-eye daisy, is found both north and south of this region. In any event, these weeds like the northern trees have shown little tendency to invade the Great Plains, a region of high plant stress both in summer and winter.

Buffalo bur and goatsbeard, shown in Figure 6, have a greater association with the climate of the Great Plains. The former, a native weed, has migrated from the southern grassland northward to its present position. It has also migrated eastward along the Prairie Peninsula where conditions in some years closely approximate those farther west. Goatsbeard ranges northward to the prairie-forest border but shows little tendency to invade the boreal forest to the north except for sporadic occurrences. Manitoba maple (*Acer negundo*) has a similar range as goatsbeard extending from the southern grassland to the boreal forest.

Behavior of a weed within and out of its climatic optimum

If it is assumed that a weed's range is principally controlled by climatic factors, then providing all other factors are equal,

that weed would tend to be found in almost every habitat within its mass climatic range. That is to say, a weed adapted to the boreal region, for example, would be found invading many kinds of habitats short of the closed forest community itself. In northern Wisconsin, buttercup is capable of invading wooded openings and is found almost everywhere. In North Dakota, however, Stevens (1946) states that this plant has been only occasionally collected along railways but is not established. This state, of course, lies in the grassland (climatic region IV shown in Figure 8). Moreover, the same author states that velvet leaf has frequently been introduced into the state but has never become established. It may be argued that velvet leaf is a weed of corn fields and hence would be restricted to the corn belt of the Prairie Peninsula. The plant is a field weed in southwestern Ontario where corn is grown farther north than the range of the weed in that province. Great ragweed in southern Wisconsin is capable of invading river bottoms as well as cultivated fields, pastures and waste places. North of this region of mass distribution, great ragweed is very sporadic and is almost exclusively found in waste places.

The behavior of a species at the edge of its range has been studied by some workers. Griggs (1914) found that some plants are extended by areas of cultivation at the edges of their ranges. The potential range of a species has been dealt with by Good (1931). While it is not denied that a weed may have a very wide potential range, what is the behavior of the plant outside its climatic optimum provided the climate is the factor responsible for its mass range? In this regard, there is the idea of peripheral selectivity of a plant at the edge of its range: *i.e.*, the plant may prefer and select a habitat which will compensate for the loss of one or more factors operating within its main geographic range. As Rubel (1935) puts it, there can be a replaceability of ecological factors. Pesola (1950) has shown that some plants in Finland show a greater preference for lime at the edges of their ranges than in their centers of distribution.

Some weeds used in this study, appearing sporadically out of their areas of mass range, show some preferences for these "unusual" habitats. Great ragweed has already been cited as one example. This weed is almost always found in waste places north of its main center of distribution. Goatsbeard, although growing well in grass sod in southern Manitoba, is almost exclusively confined to sandy soils and waste places such as railway tracks in eastern Ontario. There are many other examples of this peripheral selectivity effect. Russian thistle (*Salsola kali* var. *tenuifolia*) is an example of a weed well-adapted to the dry conditions of the grassland yet is virtually restricted to waste places out of it. It may be that the soil and the microclimate of such waste places closely approximate prairie conditions. This fact is certainly worthy of more study since control measures may be entirely different outside the main geographic range of a weed. It would be useless, for example, to attempt control of great ragweed in southern Wisconsin because of the great abundance of the weed there. In the northern sections of the state where the weed is found in waste places, control should be more feasible. Likewise, a weed such as goatsbeard, which favors sandy soils out of its mass range, should be closely watched for in sandy land and control immediately enforced when an invasion occurs.

Prediction of weed ranges from climatic data

It has been previously shown that weeds such as buttercup reaching their greatest abundance north of the prairie-forest border tension zone range far north into Canada and seem to show little tendency to invade the more arid grassland. Similarly, weeds like goatsbeard are more "at home" in the prairies and

are sporadic in occurrence in eastern North America. In these cases and others used in this study, it seems possible to predict the range of a weed providing the distribution of the plant in question is controlled by climate. For example, orange hawkweed was originally an alpine species in central Europe ranging northward into Scandinavia. Thus, in its native home the plant appears to prefer a cool, moist climate much as it does at present in North America. Since its present distribution in North America is north of the Prairie Peninsula (see Figure 5), it can be predicted that the plant may eventually occupy the agricultural areas north of the prairie-forest border. This seems to be the case since information received from the state of Minnesota indicates orange hawkweed is migrating in a northwesterly direction from adjacent counties in northern Wisconsin. As further proof that this weed favors a colder climate, it is also found in the mountains of Colorado.

It is interesting to note that it is possible to predict the locations and habitats of some weeds at present largely confined to southern Wisconsin. In the case of great ragweed and velvet leaf, the writer suspected that these weeds would be found in southwestern Ontario growing in all kinds of habitats. This portion of Ontario, like southern Michigan and Wisconsin, has a favorable climate for these particular weeds. In a weed survey of southwestern Ontario recently completed, these weeds were found in almost every kind of habitat in the extreme southern tip of Ontario which included crops, pastures, and waste places. It was also thought that if goatsbeard were found on this survey it would be growing in sandy soils. This fact was also confirmed. Although this plant has probably not yet reached its eastern limit of range, the weed's eastern extension will likely be in sandy soil. Other weeds having their areas of maximum occurrence in southern Wisconsin were also present in abundance in southern Ontario giving great trouble as weeds in both regions. Chicory and wild carrot (*Daucus carota*) are examples of such plants.

In general then, weeds whose limit of spread is controlled by climate will give the most trouble as weedy plants within the optimum climatic environment controlling their mass range. In such climatic zones control will be difficult since the plant will tend to occupy every disturbed habitat open for invasion. On the other hand, out of such a climatic zone control will be much simplified. In some cases it might be ignored completely since the weed will never become a problem but may occur sporadically from time to time only to be "knocked out" by unfavorable climatic seasons. If the weed favors some certain soil type or microclimate out of its mass range, control will still be an easy matter. Prairie weeds, for example, should be watched for in sandy soils and local areas of low humidity in eastern North America.

In conclusion, it should be said that weeds provide a fertile field of research for the plant ecologist. Not only would such investigations yield valuable practical information useful in weed control but also fundamental knowledge applicable to all phases of plant ecology. It should be emphasized, however, that there remains a great need for more taxonomic and genetic studies on weeds. Without such information, ecological investigations are seriously handicapped.

Summary

1. A rapid method for making weed surveys has been described from which can be derived frequency data for a species. This method involves the recording of presence or absence of a weed over a tenth of a mile interval while travelling by automobile. Ten such recordings were carried out for each country surveyed along a route travelled from southern Wisconsin across the prairie-forest border ecotone into the northern sections

of the state. Frequency values were then calculated for each species from the number of times the weed was found in the ten county surveys.

2. It was shown that some weeds had regions of maximum occurrence in either the northern or southern regions of Wisconsin and that their general mass ranges along the prairie-forest border and in the Prairie Peninsula made distinctive patterns. Climate of Wisconsin and the neighboring states was also investigated. The investigation included the calculation of the mean daily evaporation for July from a formula derived by Penman (1948). It was shown that the climate of northern Wisconsin was distinctly different from that of southern Wisconsin and that the latter region was one of greater plant stress both in winter and summer. It was concluded that climate was the principal factor influencing the mass ranges of some weeds in Wisconsin, in the adjacent Prairie Peninsula, and along the prairie-forest border.

3. A discussion of these weed ranges revealed that some native trees had distributions similar to the weeds.

4. It was shown that weeds whose ranges are controlled by climate tend to be present in all kinds of habitats within the optimum climatic conditions for a particular species. Out of the optimum conditions a weed may favor a habitat where local factors such as soil type or microclimate may compensate for certain unfavorable climatic conditions. A discussion of the possibility of different control measures being used within and out of a weed's climatic optimum has been given and it was shown that some weeds appear only sporadically out of their mass range, thus rendering control an easier task in such cases.

5. It was also shown that the ultimate range of a weed's mass range could be predicted from climatic data. For example, it was shown that some weeds distributed in southern Wisconsin were also present in southern Ontario since the climates of these regions are similar.

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EFFECTS OF TEMPERATURE AND PARASITE DENSITY ON THE RATE OF INCREASE OF AN INSECT PARASITE[1]

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Under favorable circumstances, most insect parasites reproduce more rapidly than their host species. Many laboratory and a few field experiments indicate, however, that the rate of increase of an entomophagous insect is closely controlled by, among other factors, the density of the host species that it is attacking. A previous laboratory study (Burnett 1951) indicated that the rate of increase in parasitism caused by the chalcid *Dahlbominus fuscipennis* (Zett.) varied inversely as the density of its host, the cocoon of the sawfly *Neodiprion sertifer* (Geoff.). In addition, the numbers of hosts parasitized, the numbers of parasite eggs laid, and the rate of change in parasitism were greatly modified by changes in temperature.

The rate of increase of an insect parasite may also be modified by variation in the density of the parasite itself. This appears to be caused by two factors. The density of the parasite population determines the number of hosts, at any given host density, that escape attack, and thus the density of the remaining hosts has a strong effect on subsequent parasite increase. Also, the density of parasites affects the effective rate of oviposition and survival of progeny through the factors of competition among adults while ovipositing and of competition among larval forms as a result of superparasitism. Through a study of superparasitism various authors have examined the relation between parasite density and (a) mortality of parasite progeny and (b) host survival. Salt (1936) examined the relation between parasite density and the effective rate of reproduction of the chalcid *Trichogramma evanescens* Westw. He found that as the density of parasites in a fixed population of hosts was increased, there was an increase in superparasitism and that, along with other effects, the number of parasite progeny reached a maximum and then decreased. DeBach and Smith (1947) studied the effects of variation in the density of the parasite *Nasonia vitripennis* (Wlkr.) on the rate of change of populations of the parasite itself and of populations of its host insect, *Musca domestica* L. They concluded that the higher the parasite density in relation to that of the host, the greater, up to a certain point, will be the total increase of the parasite population. Above this point there may be a decrease in total parasite progeny because of competition and overlapping in the search for hosts and because of superparasitism. In a paper (in Japanese with English summary) Utida (Entomological Laboratory, Faculty of Agriculture, Kyoto Imperial University) has examined the effect of parasite density on the interaction of the azuki bean weevil, *Callosobruchus chinensis* (L.), and its parasite, *Neocatolaccus mamezophagus* Ishii and Nagasawa. He found that there was an increase in parasite progeny with increase in parasite density but beyond a certain high density the number of parasite progeny remains constant. In the study mentioned above (Burnett 1951), dealing with the effects of temperature and host density on the rate of increase of *D. fuscipennis* when searching for cocoons of *N. sertifer*, a constant number of parasites searched for a constant num-

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ber of hosts distributed over various areas. The host density, and consequently the density of the parasites also, was decreased by enlarging the area over which the host was distributed. Variation in parasite density, considered from this point of view, appeared to have little effect on the effective rate of increase of the parasite population. This probably resulted because small areas were used in the laboratory experiments and because each female apparently attacked only one host.

In this paper the effects of variation in temperature and parasite density on the rate of increase of the insect parasite *D. fuscipennis* when it is searching for cocoons of its host, *N. sertifer,* are examined.

The technique used was essentially similar to that used in the host-density and temperature study previously reported (Burnett 1951). Twenty-five cocoons of *N. sertifer* were uniformly distributed, in the experimental cages, in a 5-by-5 pattern over 50 square inches of damp moss. Eight different numbers, *i.e.,* 2, 4, 9, 16, 25, 36, 49, and 64, of adult females of *D. fuscipennis* were allowed to search, in darkness, for host cocoons for 24 hours. In each experiment the eight parasite densities were used simultaneously to reduce experimental error. Each experiment was replicated ten times. The experiments were conducted at temperatures of 16, 20, and 24° C.

Parasitism of the Host

The average numbers of cocoons of *N. sertifer* parasitized by females of *D. fuscipennis* when searching at eight densities and three temperatures are given in Table I, and shown in Figure 1. The standard errors are listed in Table I, and in the following three tables, simply to show the magnitude of the variation in the results. With increasing parasite density the numbers parasitized increased throughout the range of parasite densities. Parasitism rose rapidly, with increase in parasite density, at the lower parasite densities. It increased more slowly with further increase in density until, at the highest densities, the rate of increase was more or less constant. It is remarkable that even at the highest parasite density only 80 per cent of the hosts were attacked at 24° C. At most parasite densities, the lower the temperature the fewer the number of hosts parasitized. The values obtained in the present study seem, by interpolation, somewhat lower, at comparable temperatures, host densities, and parasite densities, than those obtained in the study on the effect of host density. This was because the host cocoons were not as readily attacked by the parasite since, in the

Table I. *Numbers of* N. sertifer *parasitized by various numbers of* D. fuscipennis *when searching, at three temperatures, for 25 hosts distributed over 50 square inches*

No. of parasites	Mean number of hosts parasitized		
	16° C	20° C	24° C
2	0.40±0.163	1.50±0.166	0.80±0.200
4	2.30±0.153	3.00±0.258	3.70±0.448
9	3.60±0.221	5.10±0.314	6.80±0.442
16	5.40±0.266	7.60±0.400	9.30±0.401
25	7.10±0.277	9.70±0.300	12.10±0.482
36	8.90±0.482	11.30±0.448	13.90±0.674
49	10.90±0.526	13.40±0.542	16.70±0.716
64	12.80±0.359	15.10±0.586	19.40±0.686

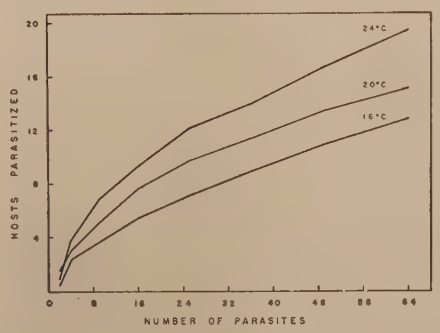

Fig. 1. The numbers of *N. sertifer* parasitized by *D. fuscipennis* when varying numbers of the parasite were searching, at 16, 20, and 24° C, for 25 cocoons of the host distributed over an area of 50 square inches.

TABLE II. *Numbers of eggs laid by various numbers of* D. fuscipennis *when searching, at three temperatures, for 25 hosts distributed over 50 square inches*

No. of parasites	Mean number of eggs laid		
	16° C	20° C	24° C
2	7.50 ±3.175	25.10 ±3.096	13.90 ±3.843
4	36.50 ±3.290	54.30 ±3.540	51.30 ±7.865
9	68.00 ±5.998	113.50 ±14.069	144.90 ±9.677
16	113.20 ±9.283	167.30 ±17.567	177.50 ±11.826
25	147.00 ±8.362	213.00 ±16.349	268.10 ±17.221
36	193.40 ±17.840	275.80 ±23.587	416.90 ±17.989
49	265.00 ±25.882	364.40 ±41.744	541.70 ±28.019
64	358.10 ±23.245	417.70 ±38.746	712.60 ±40.318

study on the effects of parasite density, they had been held in storage for a longer period.

The average numbers of eggs laid by *D. fuscipennis* when searching at three temperatures and eight densities are recorded in Table II and shown in Figure 2. With the exception of the lower three parasite densities the number of eggs laid tended to vary directly with the parasite density. At 16 and 20° C the increase in parasite eggs was not proportional to the increase in density. The curve for the experiments at 24° C is not as smooth as the other curves in Figure 2 or as those in Figure 1 but the slope of this curve approaches unity. At the lower parasite densities the relation between eggs laid and density is slightly curvilinear. At most parasite densities the lower the temperature the fewer the number of parasite eggs laid.

Table III gives the average numbers of eggs laid in the hosts parasitized at the eight parasite densities and the three temperatures. In general, at the lower five parasite densities and at the three temperatures the eggs per parasitized host were approximately equal in number and were of the same order as in the host-density study. At the higher parasite densities, with increase in parasite density there was usually an increase in the number of eggs laid in the parasitized hosts. At any given temperature, the difference between the shape of the curve for the number of hosts attacked (Fig. 1) and that for the number of parasite eggs laid (Fig. 2) resulted from oviposition by more than one female parasite in the same cocoon.

The effect of increasing density and temperature on the oviposition of the average female parasite is shown in Table IV. At all temperatures more eggs were usually laid at the lower densities than at the higher ones. At 16 and 20° C the decrease in the number of eggs per female was a little less than one-half. At 24° C there was little change in the interval 16 to 64 parasites and this followed, of course, from the curve for these experiments shown in Figure 2. At any one density the values for 20° C were less than those for 24° C, and similarly those for 16° C were less than those for 20° C.

Although the values given in Tables III and IV for the lower densities at 24° C are irregular, they may be used to estimate the effect of temperature alone on the oviposition of *D. fuscipennis* in the experimental cages. When 300 female parasites were allowed to oviposit individually on host cocoons in glass vials (no density effect) at 24° C, 242 laid 4646 eggs. Therefore, 80.6 per cent of the females oviposited, the average number of eggs per parasitized host was 19.20, and the average number of eggs per female parasite was 15.48. These

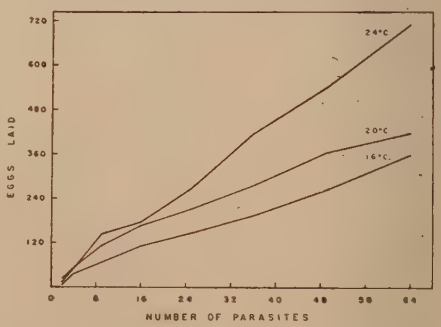

FIG. 2. The numbers of parasite eggs laid by *D. fuscipennis* when varying numbers of the parasite were searching, at 16, 20, and 24° C, for 25 cocoons of *N. sertifer* distributed over an area of 50 square inches.

values are somewhat lower than those recorded under similar conditions in the host-density study. The lower values were probably caused by longer storage of the host cocoons. The number of eggs per parasitized cocoon, 19.20, was of the same order as the values recorded at the lower densities in Table III. The number of eggs per female parasite, 15.48, approximated the values recorded at the lower densities (at 24° C) in Table IV, although these latter values may be lowered somewhat by the effect of host density. It seems, therefore, that the values obtained at the lower parasite densities and the given host densities can be attributed to the effect of temperature, for the most part, but that the effect of temperature is greatly modified by increased parasite density.

Relation between Parasitism and Parasite Density

At the lower parasite densities, the numbers of hosts parasitized at all three temperatures increased rapidly with increase in parasite density. With further increase in density they increased less rapidly until they tended to vary directly with the density of adult parasites. In Table V the values obtained, for 16 and 24° C, at the lowest six densities were compared with those derived from the simple formula

$$y = a + b \ln x,$$

where y = the number of hosts parasitized, $\ln x$ = the natural logarithm of the number of parasites, and a and b are constants. There are small systematic differences between observed and calculated values—the observed values being less at the lower and higher densities and greater at the medium densities. However, the general trend of the experimental results is similar to that of the calculated values. In this case, at the lower densities, the rate at which hosts were found by *D. fuscipennis* in these experiments varied approximately inversely with parasite density and at the higher parasite densities it became more or less constant.

The numbers of parasite eggs laid at all three temperatures may be considered to have a linear relationship to parasite density in view of the great variability in the means recorded in Table II for the lower parasite densities. At all three temperatures, however, there is a systematic trend toward a curvilinear relationship at the lower densities. The left-hand portions of the curves shown in Figure 2 resemble a parabola. Since the curves do not pass through the origin, *i.e.*, there are low parasite densities at which no hosts would be found, the

Table III. *Numbers of eggs per parasitized cocoon, when various numbers of* D. fuscipennis *were searching for 25 cocoons of* N. sertifer *distributed over 50 square inches*

No. of parasites	Mean number of eggs per parasitized cocoon		
	16° C	20° C	24° C
2	18.75±2.994	16.70±0.742	18.21±3.592
4	15.85±0.935	19.09±1.847	13.74±1.964
9	18.78±1.046	22.33±1.015	21.68±1.321
16	21.36±1.889	22.00±2.142	19.27±0.805
25	20.69±0.769	21.82±1.246	22.12±1.098
36	22.26±2.454	23.98±1.530	29.59±1.975
49	24.19±1.969	27.10±2.812	32.11±1.300
64	28.07±1.820	27.25±1.749	36.77±1.890

Table IV. *Numbers of eggs per female laid by* D. fuscipennis *when searching, at three temperatures, for 25* N. sertifer *cocoons distributed over 50 square inches*

No. of parasites	Mean number of eggs per female parasite		
	16° C	20° C	24° C
2	9.37±1.143*	12.50±1.548	9.92±2.812*
4	9.12±0.882	13.58±0.885	14.25±2.166*
9	7.55±0.666	12.60±1.569	16.09±1.075
16	7.07±0.580	10.45±1.102	11.09±0.738
25	5.88±0.334	8.52±0.654	10.72±0.688
36	5.37±0.577	7.66±0.655	11.57±0.499
49	5.40±0.527	7.43±0.851	11.05±0.572
64	5.59±0.364	6.52±0.606	11.13±0.629

* Zero values omitted.

TABLE V. *The relation between parasitism and parasite density at the lower parasite densities*

No. of parasites	Number of hosts parasitized				Number of eggs laid			
	16° C		24° C		16° C		24° C	
	Obs.	Cal.	Obs.	Cal.	Obs.	Cal.	Obs.	Cal.
2	0.40	0.10	0.80	0.51	7.50	8.84	13.90	1.50
4	2.30	1.04	3.70	3.62	36.50	32.19	51.30	49.96
9	3.60	4.30	6.80	7.26	68.00	71.77	144.90	132.09
16	5.40	5.91	9.30	9.85	113.20	111.35	177.50	214.22
25	7.10	7.15	12.10	11.85	147.00	150.93	268.10	296.35
36	8.90	8.17	13.90	13.49	193.40	190.51	416.90	378.48

formula

$$y = a + b\ x^{\frac{1}{2}},$$

where y = the number of parasite eggs laid, x = the number of parasite females, and a and b are constants, was used for the lowest six parasite densities. The values calculated by means of this formula are compared in Table V with the numbers of parasite eggs laid at 16 and 24° C. There is fairly close agreement between the observed and calculated values at 16° C (and also at 20° C although not given in Table V). At 24° C, however, the theoretical curve gives a poor fit. This appears to be caused by the irregularities in the observed values and their effect on the values of a and b rather than on the differential effect of temperature at 24° C. In general, at the lower parasite densities, the number of parasite eggs laid tended to increase as the square root of the number of parasites and, at the higher parasite densities, it increased more slowly, but more or less constantly within the limits of the experiment.

RELATIVE EMERGENCE OF HOST AND PARASITE

A rough estimate of the effect of temperature and parasite density on the efficiency of *D. fuscipennis* at the end of one parasite generation can be made by comparing the numbers of hosts and of parasites that would emerge at the end of the experiments. This has been done in Table VI, in which the numbers of hosts and of parasites that would emerge and the ratio of parasites to hosts are given. The number of hosts that would emerge is estimated by subtracting the number of parasitized hosts (Table I) from 25, the number placed in the experimental cages. It is assumed that all unparasitized hosts would emerge as adult sawflies although in nature this would not be the case. Likewise it is assumed that all eggs laid (Table II) would de-

TABLE VI. *Ratios of parasites to hosts emerging at end of parasite generation*

No. of parasites	16° C			20° C			24° C		
	Hosts emerging	Parasites emerging	Ratio para./hosts	Hosts emerging	Parasites emerging	Ratio para./hosts	Hosts emerging	Parasites emerging	Ratio para./hosts
2	24.6	7.5	0.30	23.5	25.1	1.07	24.2	13.9	0.57
4	22.7	36.5	1.61	22.0	54.3	2.47	21.3	51.3	2.41
9	21.4	68.0	3.18	19.9	113.5	5.70	18.2	144.9	7.96
16	19.6	113.2	5.77	17.4	167.3	9.61	15.7	177.5	11.30
25	17.9	147.0	8.21	15.3	213.0	13.92	12.9	268.1	20.78
36	16.1	193.4	12.01	13.7	275.8	20.13	11.1	416.9	37.58
49	14.1	265.0	18.79	11.6	364.4	31.41	8.3	541.7	65.27
64	12.2	358.1	29.35	9.9	417.7	42.19	5.6	712.6	127.25

velop into adult parasites, for it is known that over thirty parasites are able to develop on a single host. This assumption is not entirely valid for the high parasite densities because some hosts received a very large number of eggs while others received very few. The number of hosts that would emerge became progressively less with increase in parasite density and temperature. At the lower parasite densities the fact that the emergence of parasites tended to vary as the square root of the parasite density gives some indication of the amount of competition among the adult females of the previous generation. In general, the ratio of parasites emerging to hosts emerging increases, at any one temperature, slightly less than twice with each increase in parasite density. At any one parasite density, the ratio does not quite double between 16 and 20° C, or between 20 and 24° C.

Discussion

In a previous laboratory study on the relation of host density to the parasitism of *N. sertifer* by *D. fuscipennis* the rates of increase in the number of hosts attacked and in the number of parasite eggs laid were similar. This similarity occurred because each parasitized host received, on the average, the same number of parasite eggs. In that case the reproduction of the parasite was governed by the number of hosts found. In the present study on the relation between parasitism and parasite density, the results for hosts attacked and parasite eggs deposited are not similar. At the lower parasite densities, the number of hosts discovered was similar, in trend, to the number of hosts found at the lower host densities. But with increase in parasite density the number of eggs laid tended to increase more rapidly than the number of hosts discovered because of an increase in the number of females ovipositing in a single host. At 16 and 20° C particularly the increase in eggs laid was less than the increase in parasite density and this was caused, no doubt, by competition among the adult females in ovipositing. In the present study the reproduction of the parasite seemed to be governed not only by the number of hosts found but, at the higher parasite densities particularly, by competition among the adult females.

With increase in the density of adult parasites there was an increase, within the range of densities used, in the number of parasite progeny. At 16 and 20° C the increase was less than, and at 24° C it was about equal to, the increase in parasite density. If the host and parasite densities had been higher it is probable that the graphs, shown in Figures 1 and 2, would have been more curvilinear. Similarly, if the host and parasite densities had been lower it is likely that the relationship of parasitism to parasite density would have been more linear.

At most parasite densities, the parasitism of *N. sertifer* was related to variation in temperature. The greatest differences in both the host-density study and in the present study occurred at the highest densities, and the least differences occurred at the lowest densities. Under field conditions it would be expected that variation in temperature would have its greatest effect on the number of hosts parasitized and on the number of progeny left by the parasite at low host densities and also probably at low parasite densities. Perhaps the conditions of the experiments ensured that at low densities a small number of hosts would be attacked at all three temperatures.

This host-parasite system of *N. sertifer* and *D. fuscipennis* appears suitable for use in the investigation of the effects of temperature and parasite density on the rate of increase of an insect parasite under simplified field conditions.

Summary

1. The effects of temperature and parasite density on the rate of increase of an insect parasite were studied when adult

females of *D. fuscipennis,* varying in numbers from 2 to 64, searched, at 16, 20, and 24° C, for 25 cocoons of *N. sertifer* distributed uniformly over an area of 50 square inches.

2. At the lower parasite densities, the rate of increase in hosts parasitized varied approximately inversely as the parasite density. At the higher parasite densities the rate was more or less constant.

3. At the lower parasite densities, the number of parasite eggs laid tended to vary as the square root of parasite density. At the higher densities the relationship was approximately linear.

4. With increase in parasite density, the number of eggs per parasitized host increased slightly and, except at 24° C, the oviposition rate of each female parasite decreased.

5. At most parasite densities, the lower the temperature the lower the parasitism of *N. sertifer.*

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THE INDIAN AS AN ECOLOGICAL FACTOR IN THE NORTHEASTERN FOREST[1]

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There is a popular belief that the discoverers of eastern North America found everywhere an unbroken forest of giant trees. This belief has had much support from our popular literature. In the backdrop for *The Landing of the Pilgrim Fathers,* "The woods against a stormy sky their giant branches tossed" (Hemans 1826). America's fireside poet made us aware that, "This is the forest primeval" (Longfellow 1847). It has been said that a squirrel might have gone from Maine to Louisiana by leaping "from one giant tree to the next" (Bear 1951); might have travelled from bough to bough for a thousand miles without seeing a flicker of sunshine on the ground (Adams 1935); might indeed have travelled a squirrel's lifetime without coming down out of the white pines (Peattie 1950).

The vast, virgin forest recurs constantly in the works of Parkman (1909 a, b). He pictures for us "One vast, continuous forest . . . the depths of immemorial forests, dim and silent as a cavern." He paints Verrazzano off the New England coast surveying "the shadows and gloom of mighty forests." Between the French and English colonies lay "a broad tract of wilderness, shaggy with primeval woods." There was Maine, a "waste of savage vegetation"; the White Mountains "throned in savage solitude"; the Adirondacks, a "mountain wilderness"; Lake George lying in the "wild charm of untrodden mountains and virgin forests." Frontenac's army approached Onondaga "among the dense columns of the primeval forest," and across Pennsylvania "a prodigious forest vegetation . . . wrapped the stern and awful waste in the shadow of the tomb . . . a realm of forests ancient as the world." The Saint Lawrence River rolled through the "vastness of lonely woodlands." Champlain ascended the River Wye in Ontario through "the primeval woods" and the Ottawa River through "ancient wilds, to whose ever verdant antiquity the pyramids are young and Niniveh a mushroom of yesterday."

Lillard (1947) thought the dominant feature of America at the time of discovery was the virgin woods.

Many botanists seem to share the popular belief in an unbroken virgin forest and to assume that human interference with natural succession commenced with white settlement. They appear to overlook or dismiss as unlikely the possibility of significant disturbance by the Indians. The claims of some foresters and ecologists, notably Maxwell (1910), Hawes (1923), Bromley (1935, 1945), and Gordon (1940), constitute a challenge to them and call attention to the fact that a fundamental question is still unsettled. Therefore, it seems desirable to examine the evidence further in order to improve our estimate of the Indian as an ecological factor. In this paper, attention will be largely confined to Indian activities in New England, New York, and New Jersey.

VILLAGE CLEARING

Practically all of the northeastern Indians lived in villages which varied in size and permanence. Establishment of a village involved clearing for home sites and foraging within a considerable radius for the plants and animals necessary to the Indians' way of life—foods, fiber, medicines, wood and bark for utensils, weapons, canoes, and houses and particularly for fuelwood. In short, the woodland Indian

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drew upon the forest for a great variety of products (Densmore 1927, Speck 1938, Speck and Dexter 1951).

The temporary dwellings of a nomadic family band might be accommodated by a small partially-cleared area, while semi-permanent villages occupied clearings of considerable magnitude. In the Iroquois country, stockades sometimes enclosed as little as 2 acres and sometimes were 767 paces in circumference. Land outside the stockade was often cleared and occupied, the entire village site covering as much as 100 or 150 acres (Parker 1920).

Undoubtedly many village sites are still undiscovered, but archeologists have found hundreds in New England, New York, and New Jersey (Parker 1920, Willoughby 1935, Cross 1941). Knowledge of the village sites in an area is clearly fundamental in studying disturbance of the forest.

Fuelwood Cutting

Beyond the village and fields, the Indian women carried on a never-ending search for fuelwood (Lafitau 1724). Although the small dead and down trees, sometimes referred to as "squaw wood," may have been picked up first, it is probable that live standing trees were systematically cut. This is probable because an Indian village used a large amount of firewood and exhaustion of the local supply meant moving the village (Williams 1643, Mather 1702, Lafitau 1724, Loskiel 1794). So important was firewood in Indian economy that the Narragansetts of Rhode Island thought the English had come to America because they lacked firewood at home (Williams 1643).

The prodigal use of firewood by the Iroquois and Delawares, which shocked Loskiel (1794), suggests that they had a more substantial supply than dead and down trees and makes it likely that they would make use of all the wood they could obtain nearby. Lafitau's statement that the longer an Indian village was occupied, the farther the forest receded from it clearly indicates that all trees were cut. Settlers found the site of Boston so clear that they had to go to the islands in the harbor for fuelwood (Bromley 1935).

The Indians knew how to fell trees with stone axes and fire (Sagard 1632, Lafitau 1724, Kalm 1770, Waugh 1916). Some doubt may exist concerning the ability of Indian women to clear the primeval forest, but it appears that the men commonly cut the trees and left only the splitting and carying to the women (Lafitau 1724, Parker 1910), although Indian women themselves were capable axe-wielders (Eastman 1902).

Agricultural Clearing

Although considerable dependence was placed upon hunting, fishing, and collecting wild plant foods, the practice of agriculture was widely dispersed over the Northeast.

The northern Algonkians were hunters, but in the early seventeenth century, Champlain found the tribes along the Ottawa River and around Lake Nipissing growing a little maize, an art which they probably learned from the neighboring and friendly Hurons (Hunt 1940). The Montagnais-Naskapi also, who even now live by the chase (Speck 1935), were growing maize in 1634 (Thwaites 1896). By 1535, the Iroquois had pushed maize culture down the Saint Lawrence Valley as far as Quebec (Anon. 1600). In the next century, they had retreated from this region, and, according to De la Chesnaye's memoir of 1697, the nomadic Alkonkians were pointing out to the French colonists young forests arising on former Iroquois village sites (Bailey 1933).

Waugh's (1916) supposition that agriculture was practiced in the Maritime Provinces rests on Verarzanus' (1582) rather vague statement that the savages towards "Penobscot Bay and Newfoundland" were "ruder and less agricultural" than those to the southward. Verarzanus, however, was not attracted by the northern coast of North America, and

he does not appear to have examined it in detail. At the mouth of the Saint Lawrence River, Cartier (1580) saw no signs of agriculture and around Chaleur Bay only trees and "wilde corne," which was probably wild rice. Champlain (1613–32) knew the Souriquois of Nova Scotia and the Etchemins of Sainte Croix and Penobscot Bay as nomadic hunters and fisherman. Eckstorm (1945) called the Etchemins "sea-faring, tide-dwelling Indians, expert canoe-men, hunting principally the porpoise and the larger fishes." Neither Champlain nor Smith (1616) found maize fields along the coast northeast of the mouth of the Saco River, nor did Waymouth see any along the lower Saint George River (Rosier, 1605).

Champlain learned that maize was being grown in the interior in 1605 and had been grown at the mouth of the Kennebec River until enemy raids made it unprofitable. Its abandonment may have been recent, as Smith observed that along the Kennebec "where the Salvages dwelt there the ground is exceeding fat and fertill." Perhaps as a consequence of this move, the eastern Indians were raiding the coasts of Massachusetts for maize shortly after the arrival of the Pilgrims (Bradford 1898). There are other indications that the Saco River was not always the northeastern limit of agriculture on the coast. The vicinity of Mattawamkeag and Old Town, on the Penobscot River, was cultivated early (Eckstorm 1945), and in 1776, Pownall recorded that there were "old worn-out clear Fields," extending down river 4 or 5 miles from Old Town.

In southern New Hampshire, the Pennacooks apparently shared the semi-agricultural culture of the southern New England tribes (Speck 1928). Explorers found agriculture generally practiced along the coast from the Saco River southward, and Smith (1616) noted enthusiastically that the coast of Massachusetts "shewes you all along large cornefields" and that there were "many Iles all planted with corne." Pring (Anon. 1625) observed Indian "gardens" on Cape Cod, one an acre in extent.

The many fields, which the first settlers found after the plague had nearly exterminated the tribes around Massachusetts Bay, attested the extent of Indian agriculture in this region. *The Planters Plea* stated that the plague had left "in many places, much cleared ground for tillage" (White 1630). The Reverend Higgeson (1630), a resident of Salem, was more explicit: "I am told that about three miles from us a man may stand on a little hilly place and see divers thousands of acres of ground as good as need be, and not a tree in the same." Although this is hearsay, it is substantially confirmed by the appended letter of the engineer, Graves, who reported "open plains, in some places five hundred acres, some places more, some lesse, not much troublesome for to cleere for the plough to goe in."

In 1602, Edward Winslow and Stephen Hopkins found both sides of the Taunton River "for the most part cleared. Thousands of men have lived here which died in the great plague" (Willoughby 1935). These were the Pokanokets. The populous Narragansetts were also agricultural (Williams 1643), as were the Indians of Connecticut (Trumbull 1797). Southern Massachusetts was cultivated by the Nipmucs (Pynchon 1856, Speck 1928) and the Connecticut River Valley as far north as Vernon, Vermont, and Hinsdale and Winchester, New Hampshire, by the Pocumtucks (Hurd 1886, Sheldon 1895).

Northern New Hampshire and Vermont were more thinly settled, but some clearing for agriculture took place. The Cohass Intervales in the upper Connecticut Valley may be cited as an example. The first settlers found them nearly clear as the consequence of intermittent cultivation. Three or four separate clearings took place within historical times, namely, about 1628 by Mahicans from the Hudson Valley, possibly again in mid-century by Pennacooks, in 1704 by an unidentified band, and after 1725 by the

Pequawkets (Crockett 1921). The Indian name of the Intervales is striking testimony of its history—*koasuk,* the place of *little* white pines (Laurent 1884, Masta 1932).

The New England tribes in general "cultivated large quantities of maize, beans, pumpkins, and tobacco" (Mooney and Thomas 1906), and their clearings were probably responsible for the "many rich and fruitful spots of land . . . without trees or stones, near the banks of great rivers" in the New England which Hubbard (1815) knew.

The earliest observer of western Vermont and the Adirondacks was Champlain, who accompanied a war party down Lake Champlain in 1609. His Algonkian allies told him that the valleys on the Vermont side of Lake Champlain were cultivated by the Iroquois, but the war party did not actually encounter the Iroquois until it reached the vicinity of Ticonderoga. Champlain may have misunderstood his informants, who may have referred to a temporary cultivation by the Iroquois during their retreat from the Saint Lawrence sometime after 1541 (Fenton 1940).

Champlain also thought the Algonkians said that the Adirondack Mountains were thickly populated, but the paucity of archeological remains in this region suggests that the reference may have been to the proto-historic village sites in Jefferson and Fulton Counties. The Iroquois do not seem to have occupied the Adirondacks, although hunting and fishing camp sites are known (Parker 1920). Pownall (1776) could obtain no information about the region, but it is probable that the Indians were less ignorant than unwilling to give information about a favorite beaver-hunting ground.

Historians of New Netherland made frequent allusions to the agriculture of the Hudson River tribes. They mentioned large treeless flats "of seven or eight leagues and less" (Anon. 1851) and "very fine flats and maize lands" which had "few or no trees" (Anon. 1856). Henry Hudson bought maize from the Indians below the site of Poughkeepsie, New York (Juet 1610), and near Hudson, New York, he saw a bark storehouse containing "a great quantity of maize and beans" and drying beside the house "enough to load three ships, besides what was growing in the fields" (De Laet 1625). In 1636, the location of several maize fields along the River were noted by DeVries (1655). According to Jogues (1851), the first settlers around Albany used fields which had been cleared and abandoned by the Indians.

In 1626, Long Island, Staten Island, and the land between the Hudson and Hackensack Rivers were occupied by Indians who supported themselves by planting maize. Manhattan had good land on the north side, and on the east side there was a level field of 140 to 160 acres in such condition that it could "be ploughed without much clearing." The good land on the east side of the River above Manhattan "where formerly many people have dwelt" had been abandoned following war with the Wappingers (Rasieres 1628?).

It is probable that the first white men on the scene here and elsewhere underestimated the amount of land which had been cleared by the Indians. This is suggested by Van der Donck's (1656) statement that, although there were large meadows in New Netherland, there would be "much more meadow ground" but for its quick reclamation by woods. More than once he was unable to recognize as former Indian cornfields land which had been out of cultivation only 20 years.

The Iroquoian tribes placed great dependence on agriculture (Parker 1910, Waugh 1916). At one time they grew maize, beans, squashes, sunflowers, artichokes, and tobacco, and soon after contact with the white men they were raising many European fruits and vegetables and even hogs. Early observers made numerous references to their large fields and caches of stored produce. In On-

tario their fields were so extensive that when the missionary Sagard (1632) travelled from village to village, he lost his way in the fields more often than in the woods. Champlain (1613–32) traversed 60 to 90 miles of this region and called it "a well-cleared country." The peninsula between Lake Huron and Georgian Bay was mostly cleared.

Among the Mohawks of New York State, the unknown author of the journal of 1634 (Anon. 1895) ate baked pumpkins and observed in some houses more than 300 bushels of stored maize. The military expedition of Tracy and Courcelles in 1666 destroyed "prodigious quantities of provisions." Cornfields extended for two miles on each side of an Onondaga village near Pompey, New York. In 1696, Frontenac's army spent three days cutting the corn in fields which stretched four to six miles from the Onondaga fort near Jamesville, New York (O'Callaghan 1850).

In 1669, Galinée (1875) visited a Seneca village near Victor, New York, which stood in a clearing six miles in circumference. In 1687, Denonville's expedition destroyed a vast quantity of cached and standing corn at four Seneca villages. His estimate of 1,200,000 bushels may have been exaggerated, but ten days were required for the work of destruction (O'Callaghan 1850).

Sullivan's expedition into the Iroquois country in 1779 found an agriculture of surprising abundance. Every few miles his army stopped to destroy "a large quantity of corn" and "a great many fruit trees." After two days at Newtown, New York, the army moved on, because it would have taken too long to destroy all the crops there. The town of Genesee was "almost encircled with a clear flat, which extended for a number of miles, covered by the most extensive fields of corn, and every kind of vegetables that can be conceived." Among the Cayuga orchards, which were destroyed, was one of 1500 fruit trees. Sullivan estimated that his force destroyed corn at 40 villages which "at a moderate computation, must amount to 160,000 bushels, with a vast quantity of vegetables." About the same time, Brodhead's troops were destroying more than 500 acres of cornfields along the Alleghany River and "a great quantity of corn in New Ground" along French Creek (Cook 1887).

After the Iroquois were dispersed, the first settlers and surveyors found in some places recent clearings (Brown 1943) and in other places pineries covering older clearings (Gordon 1940).

The early Dutch historians considered New Netherland to be all the country between the Delaware and the Connecticut Rivers, so their general statements about the Indians of New Netherland seem to apply to the Indians of New Jersey. They were said to live chiefly on maize, which they had in abundance (Wassenaer 1621–31, De Laet 1625, DeVries 1655). The Indians encountered near Sandy Hook had "great store of Maiz" in 1609 (Juet 1610). Rasieres (1628?) could learn little about the Indians between the Hackensack and the Delaware Rivers because of the enmity between the tribes, but we know now that the Indians of New Jersey were agricultural even into the eighteenth century (Loskiel 1794, Brinton 1885).

Evelin's account of "New Albion" in 1648 stated that settlers might obtain from the New Jersey Indians two thousand barrels of corn (Smith 1765). At a later date, settlers found considerable cultivated land along the Delaware River (Lindeström 1925), but it remains for archeology to locate many village sites in this imperfectly known area (Cross 1941).

It appears probable that early writers saw only a small part of the agricultural clearing in the Northeast. Fields were abandoned as they wore out or as the white settlements came close. These abandoned fields grew up to forests. Occasionally expeditions striking at centers of Indian population saw Indian agriculture as it was, as when General Wayne

reached the village of the Miamis and their allies in 1792 and found a continuous planting the whole length of the Maumee River from the present site of Fort Wayne to Lake Erie (Mooney and Thomas 1906).

Fire

The Indians of the United States commonly fired the forests and grasslands. Indeed, Hough (1926) regarded fire as a hunting aid used by primitive peoples generally. Information on Indian burning in the western part of the country has been summarized by Stewart (1951). He found numerous reasons for burning: driving game, improving visibility, facilitating travel, driving away reptiles and insects, increasing the supply of grass seeds and berries, and for offense and defense in war. Burning was commonly practiced in the Central States (Loskiel 1794, Carver 1796, Michaux 1803, Ashe 1808, "New Yorker" 1835, Gray 1884, Shaler 1884, Marsh 1885, McClure 1899, Wislizenus 1912, Blane 1918, Shantz 1924, Bakeless 1950) and in the Southeast (Maxwell 1910, Swanton 1928).

The earliest travelers observed burning along the coast from Florida to New Hampshire. At Roanoke, Drake's chronicler noted that fires "are very ordinary all alongst this coast, even from the Cape of *Florida* hither" (Biggs 1600), Verarzanus (1582) saw "verie great fiers" along the Carolina coast in 1524, and at Roanoke, White's (1600) expedition, following a smoke, found no sign of man. At another fire, they found only "grasse and sundry rotten trees burning." Percy (1625) saw fires set by Indians on the south side of Chesapeake Bay. This may well be the explanation of the forest of "trees without underwood, and not standing so close but they may anywhere be rode through" which "An American" (1775) observed in Virginia and Maryland. Fire-hunting was a trait shared by the Carolina, Virginia, and Potomac Indians (Flannery 1939), and Smith (1625) has left us a good account of its use by the Virginia Indians. Inland, fires were common east of the mountains, and more than 1000 square miles of burned, treeless land in the Shenandoah Valley stretched northward into Pennsylvania (Maxwell 1910, Bakeless 1950).

Hudson's crew saw "a great Fire" on the shore somewhere south of Sandy Hook (Juet 1610). In 1632, DeVries (1655) smelled smoke from fires, set by the New Jersey Indians to improve their autumn hunting, even before he could see land. Smith (1765) recorded the practice of fire-hunting in New Jersey, and Budd (1685) wrote of New Jersey. "The *Trees* grow but thin in most places, and very little Under-wood." Standing alone, this statement would permit only surmise as to the cause of these open woods, but Denton (1670) and Lindeström (1925) link them to the annual burnings by the Indians. Denton reported that between the Raritan and the Delaware Rivers, there were "but a few Indians," "stately Oaks" with "broad-branched-tops" and "grass as high as a mans middle, that serves for no other end except to maintain the Elk and Deer, . . . then to be burnt every spring to make way for new." Lindström noted the abundance of thin, loosely-rooted high grass and the trees which "stand far apart, as if they were planted" and observed the firing of the dry grass to open the spring hunt. The Lenâpé Indians continued to burn the woods deliberately in the spring and fall and accidentally at other times after they had left New Jersey (Loskiel 1794). The New Jersey woods were still being burned in 1748, although Kalm's (1770) reference was probably to fires set by leaf-burning white settlers. Several observers have attributed the dominance of pines in southern New Jersey and the dwarfed growth of the "Plains" to these fires (Pinchot 1899, Stone 1911, Lutz 1934, Moore 1939).

The journals of early observers give us a rather clear picture of Indian burning along the coast of southern New England. In 1524, Verarzanus penetrated 15

to 18 miles inland from Narragansett Bay and observed "open plains twenty-five or thirty leagues in extent, entirely free from trees or other hindrances" and forests which "might all be traversed by an army ever so numerous" (Verarzanus 1582).

In 1602, Brereton (1602) remarked that the trees on Cuttyhunk grew "distinct and apart . . . upon greene grassie ground." The next year the Indians set fire to the woods on Cape Cod where Martin Pring was cutting a cargo of sassafras "which we did behold to burne for a mile space" (Anon. 1625). In the early days of the Plymouth colony, two men, becoming lost, wandered onto a "place where the Savages had burnt the space of five miles in length" (Anon. 1626).

Two early witnesses of burning in the Massachusetts Bay area wrote at some length.

> The Salvages are accustomed, to set fire of the Country in all places where they come; and to burne it, twize a yeare, vixe at the Springe, and the fall of the leafe. The reason that mooves them to doe so, is because it would other wise be so overgrowne with underweedes, that it would be all a copice wood, and the people would not be able in any wise to passe through the Country out of a beaten path . . . for this custome hath bin continued from the beginninge. . . . For when the fire is once kindled, it dilates and spreads it selfe as well against, as with the winde; burning continually night and day, untill a shower of raine falls to quench it. And this custome of firing the Country is the meanes to make it passable, and by the meanes the trees growe here, and there as in our parks.
>
> (Morton 1632)

> And whereas it is generally conceived, that the woods grow so thicke, that there is no more cleare ground than is hewed out by labour of man; it is nothing so; in many places, divers Acres being cleare, so that one may ride a hunting in most places of the land, if he will venture himselfe for being lost: there is no underwood saving in swamps and low grounds that are wet . . . for it being the custom of the *Indians* to burne the wood in *November,* when the grasse is withered, and leaves dryed, it consumes all the underwood, and rubbish, which otherwise would over grow the Country, making it unpassable, and spoil their much affected hunting; so that by this means in those places where the *Indians* inhabit, there is scarce a bush or bramble, or any combersome underwood to bee seene in the more champion ground. . . . In some places where the *Indians* dyed of the Plague some foureteene yeares agoe, is much underwood, as in the mid way betwixt *Wessaguscus* and *Plimouth,* because it hath not been burned.
>
> (Wood 1634)

In the spring of 1633, the Plymouth coloney went to work clearing the woods for cornfields, "the Lord having mitigated their labours by the Indians frequent fiering of the woods, (that they may not be hindered in hunting Venson, and Beares in the Winter season) which makes them thin of Timber in many places, like our Parkes in England" (Johnson 1654).

We can obtain a glimpse of the Indians' attitude from Roger Williams' (1643) theological arguments with his Narragansett friends.

> When I have argued with them about their Fire-God: can it say they be but this fire must be a God, or Divine Power, that out of a stone will arise in a Sparke. . . if a spark fall into the drie wood, burns up the Country, (though this burning of the Wood to them they count a benefit, both for destroying of vermin, and keeping downe the Weeds and thickets?).

It is conjectural how far up the coast the practice of burning the woods extended. The writer has found no early witnesses of actual fires north of Massachusetts Bay, but there are descriptions of the kind of forest which elsewhere early writers attributed to fires. In 1607, Captain Gilbert described the trees at a point on the Maine coast—probably Point Elizabeth south of Casco Bay. They were "the most p^t of them ocke and wallnutt growinge a greatt space assoonder on from the other as our parks in Ingland and no thickett growing under them" (Anon. 1880). Richmond Island nearby had "fine oaks and nut trees with cleared land and abundance of vines which in their season bear fine grapes" (Champlain 1613–32). Along St. George's River, and inland from it Waymouth found

> good ground, pleasant and fertile, fit for pasture, for the space of some three miles, having but little wood, and that Oke like stands left

in our pastures in England. . . . And surely it did all resemble a stately Park, wherein appeare some old trees with high withered tops, and other flourishing with living greene boughs . . . the wood in most places, especially on the East side, very thinne, chiefly oke and some small young birch.

(Rosier 1605)

It seems probable that the use of fire accompanied agriculture and fixed habitations as far north as the mouth of the Saco River. If we assume that the fires used to clear fields for planting occasionally escaped, we have to look for its influence up the valleys of the principal Maine rivers and as far northeastward as the Penobscot.

Historians and ecologists have assigned considerable importance to Indian fires along the southern New England coast (Trumbull 1797, Burnaby 1798, Dwight 1821, De Forest 1851, Hawes 1923, Bromley 1935, 1945, Walcott 1936, Colby 1941, Byers 1946). They are in general agreement that fires modified the species composition of upland forests and created extensive treeless or brush-free areas.

The outstanding dissent is that of Raup (1937). He believed that the early settlers, because of their European background, could not conceive of "open park-like woods growing naturally" and therefore assumed that the Indians has created them by fire. Actually, he pointed out, "Open, park-like woods have been, from time immemorial, characteristic of vast areas in North America. Almost anywhere one chooses to look on the periphery of the great arid plains of the interior of the continent he sees this savannah or park-land extensively developed." Raup cited no evidence for his assumption that the early settlers attributed the open woods to Indian fires because of an inability to imagine naturally open woods. Of the authorities cited in this paper, DeVries, Denton, Lindeström, Morton, Wood, Johnson, Williams, Van der Donck, and Kalm were in a position to see both the fires and their effect.

The existence of open woods on the periphery of the arid plains of the interior is not evidence for the existence of similar stands in the well-watered Northeast. There is, in fact, some question about how much of the open forest in central United States is natural and how much is the result of fire. There are many references to the creation first of open woods and finally of grassland by repeated fires and to thickets and woods which sprang up when burning was discontinued. A review of these references is beyond the scope of this paper, but attention may be called to Michaux (1803), who concluded that fire caused the "spacious meadows in Kentucky and Tennessea" and probably the plains of "Upper Louisiana and New Mexico"; to Shaler (1884) who believed that fire deforested the "prairie lands in Indiana and Illinois, and perhaps of more westerly regions"; and to Stewart (1951) who has suggested that even the tall-grass prairies may have been maintained by fires since early post-glacial times.

Information about Indian burning and other Indian activities is harder to obtain for the interior of New England than for the coastal region because hostilities postponed settlement of the interior. Dwight (1821) asserted that the oak, chestnut, and pitch pine land in New England had probably been burned for over a thousand years, but his authority is not apparent. He may have been influenced by the oak openings which he had seen in western New York. Hawes (1923) thought that the effect of Indian fire was slight except in the coastal region. Bromley (1935), using the Indian population figures of Gookin (1674) quoted by Dwight, concluded that there were enough Indians in southern New England to burn over annually most of the country that was dry enough to burn. He thought this comprised "most of the southern New England region, except the Berkshire, Taconic and possibly the hilly region of North Central Massachusetts." Raup (1937) considered inconceivable, a wholesale conflagration in Massachusetts, Rhode Island, Connecticut, and southern New York every year, reasoning that it would destroy

the undergrowth, herbaceous species, and animal life if not the forest itself. He cited Whitney's history of Worcester County, Massachusetts, which "makes very few references to fire of any kind." Byers (1946) pointed out that Whitney's book was published a hundred years after the country was settled and fifty years after the passing of a law forbidding burning. Worcester County, moreover, embraced the hilly region in which Bromley had doubted the influence of Indian fires. Other histories of interior Massachusetts towns mention Indian burning and the openness of the country. Temple's (Byers 1946) history of Brookfield stated that burning made travel by horseback feasible all through the district and that "From the top of Coy's hill cattle could be seen for a distance of three miles, and deer and wild turkeys a mile away." According to Judd (Byers 1946), the first settlers of Northampton, Hadley, and Hatfield found plenty of lowland ready for plowing and mowing and rather open homesites on higher ground, "In Philip's war and in later years companies of horsemen and larger bodies of foot soldiers seem to have penetrated the woods without difficulty in every direction. . . . When some of the people of Northampton petitioned for a plantation at Squaheag (Northfield) in 1671, they stated that the Indians had deserted the place, and that for want of inhabitants to burn the meadows and woods, the underwood had increased." Annoyance with this situation may have given rise to the laws requiring "everyman to work one day a year clearing brush from the highway." It seems that there is no evidence in the early authorities for the wholesale annual conflagration of southern New England which Raup found unacceptable but only burning "in those places where the *Indians* inhabit" (Wood 1634) and outside of swamps. Frequently the fires appear to have resembled the light prescribed burns now used in some forest types (Little and Moore 1945, 1949), and there is no question about the ability of such fires to modify species composition and to create a parklike stand without destroying the herbaceous layer and the animal life. It was reported by DeVries (1655) that, in spite of burnings along the New Jersey coast, "the hills rise up full of pinetrees, which would serve as masts for ships."

In 1760, Burnaby (1798) was concerned about the protection of New Hampshire white pines from "that very destructive practice, taken from the Indians, of fire-hunting." Pierce's history of Winchester, New Hampshire (Hurd 1886) stated that prior to 1720 the Sqakheags cleared land by repeated fires and "kept quite large areas treeless for the purposes of cultivation." Recently Bromley (1945) has pieced together the ecological history of the former Hatchet Lake Reservation in the towns of Southbridge, Massachusetts, and Woodstock, Connecticut, "the last stand of Indian influence that had once been felt throughout southern New England." Bradford family tradition supplied a description of the area as it was about 1831 when the Reservation was abandoned: "the vegetation of this section was characterized by an open forest of oak, chestnut, and hickory on the slopes; white pine and hemlock in the swamps; and bushy plains and blueberry barrens on the overly drained acid-soil plateaus and hilltops." After Indian influence ceased, pine appeared on the upland.

The valleys of the Hudson River and upper Lake Champlain must be included in the area affected by Indian burnings. Van der Donck (1656) has left us a clear statement that the Indians of New Netherland regularly burned the woods in the fall and again in the spring to make hunting easier, to improve the growth of grass, and to surround game. He saw many such "bush burnings" scorch the bark of hardwoods without injuring them and go to the top of thick pine stands, especially in Rensselaerwyck about Fort Orange. Pownall's (1776) description of the pitch pine stand between Albany and Schenectady, which he saw between 1753 and 1759, strongly suggests a fire history. In 1749, Kalm attributed decrease in the ex-

tent of fir (spruce ?) forests in the vicinity of Crown Point to "the numerous fires which happen every year in the woods, through the carelessness of the Indians, who frequently make great fires when they are hunting, which spread over the fir woods when everything is dry" (Kalm 1770).

Fire was used by the Iroquois of central New York for hunting (Morgan 1904), for improving the growth of grass (Loskiel 1794), and for clearing fields (Parker 1910, Waugh 1916). Although there appear to be few early accounts of burning by the Iroquois, it is hard to explain in any other way the grasslands and open oak forests reported by Galinée (1875). Between Lake Ontario and the Seneca village near Victor, New York, the country was "for the most part beautiful, broad meadows, on which the grass is as tall as myself. In the spots where there are woods, these are oak plains, so open that one could easily run through them on horseback." Galinée also was told that this sort of country extended eastward three hundred miles and to the west and south an unknown distance, but it is very uncertain what his Iroquois informants meant to tell him. His Dutch interpreter knew Iroquois perfectly but French very little and later proved uncooperative. Brown (1943) believes that the Iroquois made large tracts of land treeless by their practice of firing the forest beyond their villages. This seems to be fully justified inasmuch as a number of travellers observed the "oak openings" of western New York about twenty-five years after the dispersal of the Iroquois. The appearance of openings near Batavia, New York, in 1805 was described by Bigelow (1876):

> Hundreds of acres may be seen together, on which there is scarce a single tree, there being at most but an oak or a poplar or two, scattered at great distances. The earth here is covered with small willow bushes, brakes, butterfly plant . . . wild grass and strawberry vines, with very young trees not more than knee-high. In many of these open grounds, a man may be seen at a distance of two miles. There are patches of trees interspersed among these open grounds. They are of the same kind as are to be met with in the neighboring country, and are of various extent. . . . Various conjectures are indulged as to the scarcity of trees; but the most probable is that it has been occasioned by the Indians repeatedly firing whatever would burn here. . . . What serves to confirm this opinion is the frequent appearance of charcoal and burnt sticks, and the abundance of young trees which are now shooting up. Wherever groves of trees are yet standing, it may be seen that they were probably protected by the interposition of a stream of water, or by the dampness of the soil where they grow.

Sutcliffe (1812) saw these areas in 1804–06 and thought that the Indians might have taken advantage of blowdowns and kept them clear by burning. Dwight (1821) saw them about the same time and agreed that fire was the probable cause. The marks of fire could be seen on older trees, and young trees were then springing up. At first, settlers thought the oak plains were inferior to adjacent maple land, but when sowed to wheat they produced more. Gordon (1940) has called attention to a modern example—a high terrace between Quaker Bridge and Onoville, New York, which according to the earliest surveyor's report, bore a pure stand of white pine, probably growing on an abandoned Indian cornfield. Repeated fires by Reservation Indians have since reduced it to a low growth of scrubby oaks and hickories.

Evidence for the deliberate use of fire by the Indians in northern New England and the Adirondacks seems to be lacking. It is noteworthy that Perrot (1864) described the use of fire for hunting buffalo on the prairies but does not mention its use for hunting moose and caribou in the North. Flannery (1939) thought fire-hunting was "not practical in inflammable forest country like the coniferous North," although we have seen that it was practiced in other inflammable forest regions. The usual incentives for burning, however, were lacking in northern New England and the Adirondacks: agriculture was less practiced; summer travel was by canoe rather than overland; winter travel

by snowshoes or on the ice was not hindered by underbrush; and deer hunting took the form of stalking or still-hunting rather than driving (Speck 1940). Only a few weeks after Kalm had described Indian burning at Crown Point, he noted that the Indians at the northern end of Lake Champlain were careful in their use of fire.

> The natives usually make a fire during the night, both summer and winter, when they camp in the woods. One would think that as a result there would be many forest fires during the summer, but I was given to understand that although at times fires do start during the summer, it seldom happens, for the natives themselves are very careful to put out the fires wherever they have made them, inasmuch as it serves their own interest. If a fire should break out and destroy the forest and the vegetation, the roe deer would flee from this region with the result that their hunting would be much less successful.

Early descriptions of this region placed more stress on the thickness of the woods than on openings. For example, Josselyn (1672) called the country north of the White Mountains "daunting terrible, being full of rocky hills, as thick as molehills in a meadow, and clothed with infinite thick woods." Irving (1803) recorded that, while returning from New York's Black River country, "We were a great part of the time passing through thick woods the underwood being so thick as to prevent our seeing to any extent." Still it is hardly to be doubted that even in northern New England and northern New York, the pyric factor was present in the form of an occasional escaped camp fire and of lightning.

Hunting Controls

The influence of the biotic factor on plants has been clearly stated (Daubenmire 1947). The existence, if not the details, of a dynamic plant-animal interrelationship is well-known, but the influence which the Indians exerted indirectly upon forest composition through their hunting activities has gone largely unnoted. The writings of anthropologists (Speck 1915, 1931, 1938, Speck and Eiseley 1939, Cooper 1939, 1946, Hallowell 1949, Speck and Dexter 1951) give us considerable insight into the thoroughness of Indian control over animal population in portions of the Northeastern woodland. Tribal land was divided into family hunting territories with definite boundaries. The proprietors of each territory knew intimately the plant and animal inventory therein, harvested the supply carefully with rituals of atonement and thanksgiving, and rotated their activities in such a way as to conserve the supply. We can hardly escape the conclusion that they maintained, as well as they were able, a balance favorable to their economy and that this was a different balance from that which would have obtained in an unpopulated country. No one seems to have attempted an evaluation of this factor on plant succession. In Bromley's (1945) observation that Indian burning in Massachusetts increased the food supply for heath hen, passenger pigeon, wild turkey and deer, the effect of animals is clearly secondary.

Favoring Food and Medicinal Plants

The Indian practice of favoring nut trees and other food plants was probably responsible for minor changes in the original forest. Bromley (1945) thought woods were burned partly for this purpose. Because nut-tree stands on village sites are usually even-aged, Baker (1950) advanced the theory that they originated when village establishment suddenly decimated the rodent population that planted the nuts. However, there appears to be an association of American chestnut, *Castanea dentata* (Marsh.) Borkh., groves and Indian village sites in lower Ontario, and Jury (1952) is inclined to the opinion that the trees were planted by the Indians. The Iroquois of New York planted the Canada plum, *Prunus nigra* Ait., and possibly Kentucky coffee tree, *Gymnocladus dioicus* (L.)

K. Koch, since it is most often found near village sites (Hedrick 1933).

Plants used by Indians for medicinal purposes may owe their existence in many localities to the transplanting hand of an Indian herbalist (Fenton 1942). Groundnut, *Apios tuberosa* Moench, and leek, *Allium tricoccum* Ait., were also cultivated (Hedrick 1933).

Evaluating the Influence of Indian Activities

We must conclude from the foregoing that the Indians of the Northeast cleared land for villages and fields, cut fuelwood and set fires beyond these clearings, exercised a wide indirect influence on vegetation through their hunting, and may have favored or even transplanted food and medicinal plants. These facts alone, however, are not very helpful in evaluating the extent and intensity of Indian influence in the Northeast or in reconstructing the history of a particular area. One needs rather full knowledge of four other factors which will be merely outlined in this paper—the duration of Indian occupation, the population density, population concentration and movements, and the local pattern of settlement or preferably the location of all village sites.

The peopling of North America began perhaps 25,000 years ago, but it did not take place uniformly and was not completed until rather late (Gladwin 1947). The age of archeological finds in the West has been placed at 6,000 to 10,000 years by radioactive carbon (Bell 1951). This kind of evidence does not seem to be available yet for the Northeast, but occupation of New England, New York, and New Jersey by a pre-Algonkian people began in very remote times (Parker 1920, Willoughby 1935). The entrance of the historic Algonkians and Iroquois into the Northeast has not been dated satisfactorily, but the Indians found in "Vinland" by the Norsemen about 1000 A.D. bore some resemblance to Algonkians (Haugen 1942). Indian traditions agree that the land had been occupied for generations before the arrival of the white men (Hale 1883, Brinton 1885, Speck 1928).

We shall never know the population of the northeastern tribes in the sixteenth century, because the white man's acquaintance with them was preceded by his diseases and his disruption of the primitive economic patterns (Ruttenber 1872, Ashburn 1947, Hunt 1940). Early statistics are fragmentary; they contain much hearsay evidence. It may be suspected that they were sometimes colored by the motives of their reporters (Gallatin 1836, Bancroft 1885). Often the observers suffered from language difficulties with their Indian informants and from confusion in tribal nomenclature. Smith (1616), for example, admitted that he wrote not fully but "as I gathered from the niggardly relations in a broken language to my understanding."

Indian populations were often reported only as numbers of fighting-men. As hostility was almost continuous along the border, this practice is understandable, but it is another source of error. The fighting-men were variously estimated as one-third, one-fourth, one-fifth, one-sixth, and one-ninth of the total population (Lahontan 1703, Trumbull 1797, Dwight 1821, Tyron in O'Callaghan 1850, Beauchamp 1892, Thwaites 1896—Relation of 1657–8, Lloyd in Morgan 1904, Crockett 1921, Brown 1943). This is not the place to survey the rather extensive literature dealing with Indian numbers. The most complete enumeration is that of Mooney (1928), but it was frankly tentative and some errors are apparent. Ecologists may feel that procuring this information is properly an enthnologist's work, but the information is indispensable for understanding the ecological history of the Northeast or specific portions thereof.

Although family groups sometimes lived apart, the Northeastern Indian population characteristically congregated in villages which were moved seasonally or

at intervals of several years. Even the nomads of Labrador gathered in villages in the summer (Speck 1935). In northern New England, the Abnakis seem to have lived in villages part of the year (Speck 1940), while in southern New England, New York, and New Jersey a more agricultural population lived in villages of some permanence.

The villages of the Abnakis went through an annual cycle of migration—southward to seashore camps for the summer, northward to deep woods hunting camps in the fall and winter, returning to villages along the rivers for late fall feasting and spring fishing and planting. Apparently the seacoast and interior tribes of Connecticut made seasonal visits to each other's location, even exchanging residences altogether (DeForest 1851). The Lenâpé had a similar pattern of movement between seashore and interior in New Jersey (Philower n.d.).

Even the villages of agricultural tribes were moved at intervals as the soil declined in fertility, as the local supply of firewood became exhausted, as weed infestation of fields, scarcity of game, or trash and vermin made the site uninhabitable (Mather 1702, Lafitau 1724, Loskiel 1794, Beauchamp 1892, 1905, Parkman 1909a, Ganong in Champlain 1613–32, MacLeod 1936, Fenton 1940, Brown 1943). Other moves were dictated by military considerations (Champlain 1613–32, Fenton 1940).

Lafitau (1724) reported the frequency of these moves vaguely as "after a certain number of years" and Loskiel (1794) as "frequently." Other estimates agree fairly well. Champlain (1613–32) judged them to take place every 10, 20, or 30 years; Beauchamp (1905) every 10 or 15 years; and Fenton (1940) every 10 years and "about twice in a generation." These estimates are confirmed by the known locations in the village of Onondaga, which was near the present Syracuse, New York. As the federal capital of the Five Nations, who were feared and courted by both France and England for over a century, Onondaga was often visited by missionaries, travellers, hostile expeditions, and political emissaries. It appears from their accounts that Onondaga occupied at least nine different sites between 1610 and 1780 (Hewitt 1928).

The tendency of the Indian population to congregate in villages and to migrate had a direct bearing upon its effectiveness as a disturber of the primal scene. It is clear that the village habit localized and intensified disturbances, while seasonal migrations and periodic relocating of villages widened their influence. It should be recognized, however, that these movements were not random. Seasonal migrations followed much the same course each year, and there was a tendency for desirable village sites to be reoccupied by the same tribe or by their conquerors.

There is no substitute for a complete knowledge of the archeology of an area in determining where Indian influence may have been operative, but our tentative conclusions may be improved by knowing the historic locations of the Indian population and the kinds of sites which were usually chosen for villages and fields. It is natural to assume that most villages were located along streams and bodies of water because of the importance of fish food and the fertility of alluvial soil. Indeed, Marsh (1885) thought these were the only village sites. Islands and land partly enclosed by stream confluences and meanders were sometimes chosen for defensive reasons. Defensive needs, however, often dictated hilltop locations. This was characteristic of prehistoric and proto-historic Iroquois villages (Fenton 1940) and probably of others. Kellogg found that village sites in the Lake Champlain Valley were often located "at a distance from any even moderately large body of water" (Crockett 1921).

While looking into the question of Indian disturbance, the writer has not emphasized the existence of large tracts of undisturbed forest. Their existence is generally accepted (Champlain 1613–32,

Smith 1616, Wood 1634, Josselyn 1672, 1675, Pownall 1776, Strachey 1849, Shaler 1884, Maxwell 1910, Hawes 1923, Willoughby 1935, Byers 1946, Bakeless 1950), although, as Gordon (1940) pointed out, it would be difficult to prove primeval status absolutely in any particular case. In fact, their existence and extent may have been accepted too readily. For example, when Hawes asserted that, "While the Indian fires may have affected the forests near the coast, there were undoubtedly great stretches of virgin forests unbroken except by the occasional river meadows," this may have been true, but we should not assume that it was true for a particular locality without a careful study of local archeology and history.

A good case in point is Vermont, which is customarily treated as having had no Indian population worth mentioning. Champlain thought that the Vermot shore of Lake Champlain was inhabited in 1609, but subseqent events indicate that he was probably mistaken. His informants may have been referring to recent transient occupation by the Iroquois. During the French and Indian wars, Vermont's position made it a no-man's land. Gallatin (1836) stated that "There do not appear to have been any tribes of any consequence in the northern part of New Hampshire, or in the State of Vermont." Ray (1943) asserted, "We know, indeed, that Vermont was wholly without aboriginal inhibitants." Gookin's (1674) editor commented that "The Indians were never numerous in Vermont." Bancroft (1885) wrote, "Vermont and northwestern Massachusetts and much of New Hampshire were solitudes." Palfrey (1882) ignored Vermont in his enumeration of the New England Indians, apparently following Gallatin. Parkman (1909a) claimed that Vermont "had no human tenants but the roving hunter or prowling warrior." Willoughby (1935) agreed "There seem to have been but few Indians in Vermont" at about the beginning of the seventeenth century. In Van de Water's appraisal, there was an unbroken forest, virginal and empty, between Lake Champlain and the Connecticut River.

It would seem that here if anywhere the original forest should be free of anthropeic influence. An ecologist in a hurry might so assume and in so doing would make a serious mistake. Crockett (1921) brought to light the little-known fact that Indians from southern New England and from Maine occupied parts of Vermont following their defeats in 1676 and 1680. The French maintained missions among them on Otter Creek and on the Winooski and Mississquoi Rivers until about 1760. There were permanent Squakheag and Missiassik settlements in the extreme southeastern and northwestern corners of the state respectively, and there were intermittent settlements along the upper Connecticut River. The Mahicans repaired annually to the Walloomsac and Battenkill valleys. The Caughnawagas, after locating on the St. Lawrence River, hunted and trapped for decades west of the Green Mountains. After listing evidence of occupation in 29 Vermont townships, Crockett concluded that such evidence had doubtless been found in every township in Vermont. This should make the ecologist wary of supposedly uninhabited regions.

Summary

The northeastern United States was occupied from remote times by an Indian population whose size has not been—and perhaps can never be—determined accurately. Most of this population lived in villages. These Indians created sizeable clearings for their villages and fields and probably expanded the clearings as they foraged incessantly for firewood and other necessary materials. Over much of the region, they set fire to the woods to improve travelling and visibility; to drive or enclose game; and to destroy "vermin." They probably exercised some inflence on the forest through their control over the animals they hunted and through

planting food and medicinal plants. It is certain that their activities destroyed the forest in some places and it is hardly to doubted that they modified it over much larger areas. Seasonal migrations and the periodic relocating of villages widened the range of Indian influence, which extended into unexpected localities and supposedly uninhabited regions.

We must conclude that an area which was wooded when first seen by white men was not necessarily primeval; that an area for which there is no record of cutting is not necessarily virgin; and that a knowledge of local archeology and history should be part of the ecologist's equipment.

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EVIDENCE FOR THE CONCEPTS OF HOME RANGE AND TERRITORY IN STREAM FISHES[1]

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INTRODUCTION

The size and structure of fish populations have received much attention in recent years. Contributions in this field have provided ideas concerning the theory of animal populations as well as a sound basis for the management of sport and commercial fishing. Among the factors influencing fish populations, most study has been accorded food, feeding habits, reproductive behavior, reproductive potential, growth, and mortality. The fish population has been considered an aggregate of animals in most studies of this sort. Very little attention has been given to the interaction between individuals of a fish population and to the effect such interaction might have on the size and structure of the group. The present work attempts to interpret a population of stream fishes as the result of competition among the individuals of which it is composed. The movements of the fish have been followed in detail and the possible importance of these activities is discussed.

Evidence will be presented to show that many stream fishes live in very restricted areas during most, if not all, of their lifetime. The movements of fish will be considered from two viewpoints: (1) home range, and (2) territory. Home range is a term borrowed from the mammalogists who have found that many mammals live within rather narrowly circumscribed limits. Such small mammals as the meadow vole, woodland deer mouse, woodmouse, and chipmunk have received most attention in this respect, but even larger species like the coyote and rabbit have shown a similar pattern though on a larger scale. Although the home range is a well-recognized phenomenon among mammals, it has been defined in many ways. Burt (1943) defines home range as "the area, usually around a home site, over which the animal normally travels in search for food." This is an acceptable definition of the term in many respects, but the element of the "search for food" is overemphasized. The main purpose of many activities may not involve the search for food. The home site implies a nest, a burrow, or some other attraction for the animal. Many animals have no such attraction during times when they are not breeding and yet confine their movements to restricted areas. For these reasons, home range will be redefined as "the area over which the animal normally travels." This is the same definition that Hayne (1949) used in his discussion of the calculation of the size of the home range.

The concept of territory had its beginnings in ornithology (Altum 1868), and the bulk of the work has been confined to these animals. The writer will use the term territory as Noble (1939) did: "Territory is any defended area." Nice (1941) accepted this definition. According to Allee *et al.* (1949), "territoriality includes homing or the defense of a given area or both." The writer believes that homing and the defense of an area are distinct phenomena, motivated by different stimuli. Noble's definition is preferred because it does not confine the idea of territory to the reproductive season, to one sex, or to animals of a specified age.

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To distinguish between home range and territory it must be emphasized that defense of a territory is the aggressive response of an animal for the protection of an area from invasion. Home range implies no aggressive action. When territory and home range boundaries coincide, the term "territory" should be used.

Aggressive behavior is very common and widespread among vertebrates (Collias 1944), and may be expected to be observed whenever the behavior of a number of individuals is studied. Burt (1943) rightly points out, however, that territoriality cannot be assumed, but that the aggressive behavior must be observed. It has not been possible to observe such behavior among the fishes in the murky southern Indiana streams, although it may be expected to occur on the basis of Greenberg's (1947) studies with the green sunfish. An experiment was designed to test this assumption in lieu of direct observational evidence.

Home range is a new concept as applied to fish behavior, but it has been realized that fishes have reproductive territories ever since the habits of nest-building fishes, particularly the sunfishes, began to be studied seriously. Breder (1936), Reighard (1920), Langlois (1936, 1937), Raney (1940) and many others have described this behavior. Territory is considered here in a more general sense inasmuch as the experiments were conducted after the main spawning period. The term "home range" will be used when the behavior of the fish can be interpreted as a response not necessarily attributable to aggressive action. Territory will be associated with responses which can be interpreted as an indication of aggressive action. Home range and territory were not sharply distinguished by the field procedure that was used.

FIG. 1. A view of section F, Richland Creek, Greene County, Indiana. Rock outcrop can be seen on the hillside. A rock face about 15 feet high, shown on the extreme right, has been exposed by stream action.

DESCRIPTIONS OF THE CREEKS

Richland Creek, a bedrock stream in Greene County, Indiana, was described in a previous paper by the writer (1950), who found its population to be stable during one summer in spite of the stress of a flash flood. Floods and high water have been typical during four years of observation. The portion of the stream selected for these studies is characterized by two main pool areas separated by a shallow riffle, 242 feet long. The extremities of the experimental area were bounded by other riffles. The site was selected because it was felt that the long riffle, designated as section D, would be a mechanical barrier to fish moving between the two pools. The downstream pool was subdivided into two sections, designated A and B, 242 and 184 feet long respectively. The upstream pool was also divided into two sections called E and F (Fig. 1), 246 and 117 feet long. The designation of section C has been changed since the previous report. This section, a 40-foot portion of the long riffle immediately above section B, has been included in section B because it has developed pool characteristics.

Stott's Creek, in Morgan County, Indiana, was investigated in order to compare the results of similar experiments of one-summer duration performed on creeks with different biological and physical characteristics. Biologically, Richland Creek and Stott's Creek were dissimilar in the species composition of the

FIG. 2. A view of section A, Stott's Creek, Morgan County, Indiana. The sand and gravel nature of the stream is illustrated by the bar at the left. The stream meanders a great deal, being deflected by abundant stream debris.

fish fauna and in the relative abundance of species common to both creeks. Physically, the two streams diverged widely. Stott's Creek flows through the broad White River Valley in glaciated country. Its gravel and sand bottom is advantageous for a distinct riffle-pool development (Fig. 2). Fallen trees, stumps and logs make the pools small and deep. The stream bed shifts greatly from year to year, but the characteristics of the pools and riffles remain relatively constant for a summer season. The pools are almost isolated during low water, but there are several opportunities each summer for fish to move because the creek rises rapidly after a moderate rain. The bedrock bottom of Richland Creek makes it much more resistant to change from year to year. Its pools are longer and in general are less well defined than the pools in Stott's Creek.

EXPERIMENT I—YEAR-TO-YEAR MOVEMENT

Design of Experiment I

All experiments to be described here have a common rationale. If fish are marked distinctively in a given section of stream and are caught in the same section at some later time, it is assumed that the fish have confined their activities to that particular section. Conversely, if a fish is found in a section some distance away from its point of original capture, it is considered to have moved from the particular section where it was marked. In the first case, the fish will be called "home" fish and in the latter case they will be called "stray" fish.

Richland Creek. The fish were marked by removing a pectoral or ventral fin. Fish in section A were marked LP (left pectoral fin removed); section B fish were marked RP; section E fish were marked LV (left ventral fin removed); RV was the mark used in section F. No difficulty was encountered recognizing missing fins as long as four years after the fish had been marked. All fish were captured with the electric fish shocker by working subsections about 60 feet long that had been blocked off by nets with $\frac{1}{4}$ inch mesh. A similar method was described by Shetter (1948), and our modification is described by Gerking (1950).

Fish were marked in late June of 1948 and an attempt was made to recapture them in early August of the same year. The area was traversed again in early July of 1949 when recaptures were sought and more fish were marked in the manner previously described. Mid-July of 1950 dated a similar operation, but individuals were not marked in that year. Late July of 1951 was the last time the stream was examined in this connection. Thus, in August of 1948, recaptures were being sought from fish marked in June of the same year. In 1949, individuals which had been marked in 1948 were sought. In 1950, the 1948 and 1949 marks were subject to recapture and the same was true in 1951. Although a different time element prevailed between the time of marking and the time recaptures were made in different years, the data are homogeneous enough for direct comparison.

A part of the data from the 1950 paper is incorporated into the analysis and in-

terpretation of results to be presented here.

Stott's Creek. The Stott's Creek experiment was planned similar to that above. The area was subdivided into four contiguous sections (A, B, C, and D). Each section contained 2 small pools separated by shallow riffles. Section A was 460 feet long; section B was 300 feet long; section C was 500 feet long; and section D was 640 feet long. Each section was at least twice as long as the Richland Creek sections.

Fish were caught by the electric fish shocker and were marked in the same way as described for Richland Creek. Marking took place July 15–22, 1949 and the search for recaptures was made August 18–24 of the same year. The Stott's Creek data will be referred to briefly for comparative purposes.

Experimental errors

Systematic errors

1. The 1950 paper pointed out that fin-clipping might influence the fish so that their movements might not be normal. The assumption that fin-clipped fish behave normally is fundamental to the interpretation of the data. To test this assumption, the movement of fin-clipped fish was compared with that of a group of fish made recognizable by an india ink tattoo mark which avoided amputation. Aquarium fish showed no harmful effects from this kind of mark, but the tattoo mark faded in three weeks. Thus, the time between marking and recapture in the field experiment was limited to two weeks.

An experimental area in Stott's Creek, several hundred yards upstream from the one already described, was divided into three sections. Fish of several species studied in both Richland Creek and Stott's Creek were captured with the electric shocker and marked distinctively in the three sections: 109 fish were fin-clipped and 69 were tattooed. Two fins were removed instead of the customary one, in order to elicit a maximum response to the effect of fin removal. A greater proportion of the tattooed fish moved, but a test of independence (Snedecor 1946) between the two classifications indicated that the difference between them could be accounted for by random sampling from a homogeneous population (Table I). As a result of this test more confidence can be placed in the assumption that the movement of fin-clipped fish is representative of normal fish.

2. There is a possibility that fish which have been subjected to an electric field behave differently than those which have not received such treatment. This source of error is subject to experiment, but an attempt to measure it was unsuccessful because of our inability to capture enough fish by netting to make the test conclusive. During the four years that the electric shocker has been operated in Indiana, no difference in behavior between shocked and normal individuals has been observed in the field, and in laboratory aquaria no behavioral differences have been noticed between fish caught by shocking and netting. Consequently, the effect of shocking on the movement of marked fish is considered to be negligible.

3. The most important error in the analysis involves the fish which have strayed completely away from the study area. These fish should be included among the strays, but circumstances prevented a thorough search for them in Richland Creek. A pool 15 feet deep was present a short distance downstream.

TABLE I. *A comparison of the movements of fish marked by fin-clipping with those marked by tattooing in 3 sections of Stott's Creek*

Type of mark	Home	Stray	Total
Fin-clip	32	3	35
Tattoo	14	4	18
Total	46	7	53

$\chi^2 = 0.884$ with 1 d.f., $p = .40$.

from the study area, and a long stretch of water 6–8 feet deep was adjacent to the upstream end of the area. A search was made below the deep downstream pool the first three years, and only one rock bass originally marked in the study area was discovered during this time.

A rough estimate of the number of fish that left the experimental area can be made from the composition of the known strays. In the extreme sections, A and F, fish could have escaped sampling by moving only a short distance. The 32 strays of all species which remained in the experimental area might have been matched by an equal number which escaped from the area by moving in the opposite direction. Those in sections B and E had to move at least twice as far to escape the sampling area. Six fish from sections B and E were known to have strayed at least two sections away from the place where they were marked, and an equal number might have escaped. But the riffles at the extremities of the experimental area could have acted as barriers to fish movement as the long riffle between sections B and E did. Seventeen of a total of 80 strays crossed the long riffle during four years of observation. This can be considered as a rough measure of the resistance of the riffle to fish movement. An estimated $32 + 6 = 38$ fish might have escaped if there had been no riffle at each end of the area, so $17/80 \times 38 = 8$ fish which might have been recaptured had they not escaped from the experimental area. This amounts to 2.5 per cent of the total number of recaptures caught during this time, which may well be an underestimate. Probably the loss of marked fish amounts to no more than 5 per cent of the number of recaptures. This unavoidable error does not affect the main conclusions of the experiment.

4. The use of arbitrary boundaries between stream sections places the investigator at a slight disadvantage because some fish might have home ranges which coincide with a boundary. These might be classed as strays even though they were exhibiting the same movements as home fish. This difficulty was unavoidable.

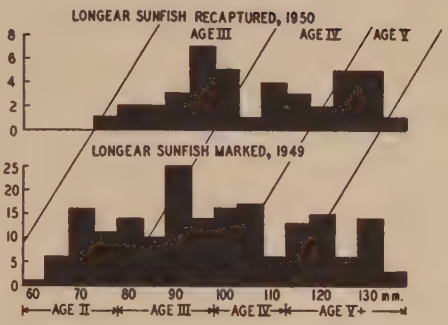

FIG. 3. Length frequency distribution of longear sunfish marked in 1949 and recaptured in 1950 in Richland Creek. Age determinations were made by the scale method on a sample of fish from the experimental area of the creek.

Sampling Errors

1. Not all species are represented by equal numbers among the fish marked and recaptured due to a difference in their relative abundance in the stream. The data to be presented are, therefore, not equally reliable for all species. In order to overcome this difficulty, the movement of each species has been analyzed statistically.

2. Since the electric shocker is not equally effective on all sizes of fish, the data are not applicable over the complete size range of a particular species. Large fish are the more easily collected. The fish marked and those recovered (Fig. 3) include an undue proportion of the older year classes.

3. It becomes more and more apparent that the electric fish shocker is not a random sampling device. Such factors as water conductivity, murkiness, depth, amount of stream debris, and persistence of the workers affect the size and quality of any sample. These factors can change from year to year or, in respect to the

workers' persistence, may change during one day's or week's operation. This error becomes important in population estimates but will not affect our observations on fish movement.

Species with restricted home range

Longear sunfish (*Lepomis megalotis*)

The longear sunfish is a very abundant, if not the most abundant, centrarchid fish in the smaller mid-western streams. It generally lives in quiet pools rather than in swift currents. Like the other centrarchids, it is a nest-building species. The main spawning is in May and June, although some breeding can be observed throughout the summer.

Richland Creek. The marked fish were distributed quite evenly in 3 of the 4 stream sections; there were fewer marks in section F because it was the shortest (Table II). Ages II, III, IV, V, and possibly a few age VI were included among the marked fish (Fig. 3). Because the size range of the different ages overlaps considerably, the age boundaries shown in the figure are arbitrary. Very few longears live more than five years, so that the five-year-old fish marked in any year have practically all disappeared from the population by the next year. By the same token, it was necessary to mark many small fish (age II), in order to insure a sufficient number of recaptures the following year.

The chi-square method can be used to test the hypothesis that the marked fish, as represented by the recaptures from all four years, distributed themselves at random throughout the area after being released (Table III). If the marked fish moved at random in the area, they could be expected to be distributed in relation to the population in each section. For each section Petersen-type population estimates (Ricker 1948) have been expressed as percentages of the total population for the whole area (the actual population size is not necessary for the analysis). The number of recaptures, associated with each kind of mark, which could be expected to occur in each section on the basis of random distribution of the marked fish, can be calculated and the χ^2 test performed. The χ^2 value of 350.41 with 12 d. f. (degrees of freedom) is far above the 1 per cent level of significance ($\chi^2_{.01} = 26.22$ with 12 d. f.). It is concluded that the marked fish did not move at random after they were released. Consistent results were obtained in the analysis of each year's recaptures.

TABLE II. *The distribution of marked longear sunfish in a 0.2 mile region of Richland Creek*

Year	Section A LP	Section B RP	Section E LV	Section F RV	Total
1948	94	123	86	31	334
1949	45	42	57	44	188
Total	139	165	143	75	522

TABLE III. *Number of longear sunfish recaptured in Richland Creek during four years*

	Population percentage	Area of recapture			
		Section A	Section B	Section E	Section F
Section A Fish marked LP	32.8	27	10	1	0
Section B Fish marked RP	28.7	11	41	1	1
Section E Fish marked LV	27.0	1	1	73	6
Section F Fish marked RV	11.5	0	0	3	15

$\chi^2 = 350.41$ with 12 d.f., $p = <.01$.

Since the marked fish did not move at random after their release, the question arises as to the nature of their distribution. There was very little interchange between the two large pool areas. Only 5 of the 191 recoveries moved across the long intervening riffle during the four years' observations. A somewhat greater interchange between sections within each of the long pool areas occurred, but by far the majority of longears were found within 100–200 feet from where they were originally marked. The concentra-

tion of recaptures diagonally across the table demonstrates that most of the fish were caught in the section where they were first found. Home fish made up 81.7 per cent of the total number of recaptures. A calculation of χ^2 for the fish in sections A and B showed that they did not move at random in the downstream pool ($\chi^2 = 27.17$ with 2 d. f., $\chi^2_{.01} = 9.21$ with 2 d. f.). A similar value of 43.01 for the fish of sections E and F shows that there would be less than one chance in 100 that this distribution could have resulted from a random movement of the fish in the upstream pool. It is concluded that the majority of longear sunfish, living in a small bedrock stream, confine their activities to about 100–200 feet.

Stott's Creek. Longear sunfish were not as abundant in Stott's Creek as in Richland Creek. Sixty-seven of various sizes were marked and 12 were recaptured one month later. Of those recaptured, 11 or 80.1 per cent remained in the same section where they had been marked. This sample compares favorably with Richland Creek. Since Stott's Creek has different physical characteristics from Richland Creek, it becomes very probable that this behavior of longear sunfish is not confined to one particular stream. The tendency for most longear sunfish to limit their activities to rather small areas may hold throughout the range of the species.

Rock bass (*Ambloplites rupestris*)

Rock bass were not as numerous as the longear sunfish in either stream. They generally live in quiet pools or around rocks and other sheltering obstructions. Rock bass construct nests and spawn principally in early spring.

TABLE IV. *The ditribution of marked rock bass in a 0.2 mile region of Richland Creek*

Year	Section A LP	Section B RP	Section E LV	Section F RV	Total
1948	22	21	25	8	76
1949	8	16	14	10	48
Total	30	37	39	18	124

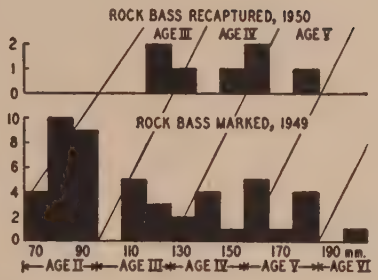

FIG. 4. Length frequency distribution of rock bass marked in 1949 and recaptured in 1950 in Richland Creek. Age determinations were made by the scale method on a sample of fish from the experimental area of the creek.

Richland Creek. Fewer rock bass were marked in section F than the other sections where the number of marks were about equal, averaging 35 per section (Table IV). Fish of ages V and VI which were marked in 1949 had disappeared from the population by 1950, presumably by natural mortality (Fig. 4).

Rock bass had the same pattern of distribution as described for the longear sunfish (Table V). The χ^2 value of 155.00 (12 d. f.) indicates that the fish did not move at random in the experimental area. Only one rock bass which had moved across the long riffle was taken in four years. The experiment demonstrated a real tendency for rock bass to remain within 100–200 feet of

TABLE V. *Number of rock bass recaptured in Richland Creek during four years*

	Population percentage	Area of recapture			
		Section A	Section B	Section E	Section F
Section A Fish marked LP	15.3	6	1	0	0
Section B Fish marked RP	56.0	1	7	0	0
Section E Fish marked LV	17.0	0	0	15	1
Section F Fish marked RV	11.7	0	1	2	0

$\chi^2 = 155.00$ with 12 d.f., $p = <.01$.

their original location from year to year. The marks LP, RP, and LV were concentrated in the section where they were first caught. Only 3 rock bass marked RV were taken and these were all strays; 2 were caught in section E and one in section B.

Stott's Creek. Nine rock bass were caught and marked in Stott's Creek. Three of these were recaptured and all 3 were found in the section where they were marked. This limited information agrees with the main conclusion above, *i.e.,* that rock bass have a restricted home range. This phenomenon seems to occur in more than one stream.

Green sunfish (*Lepomis cyanellus*)

The green sunfish reaches its greatest abundance in small bodies of standing water, and is less frequent in small streams. It spawns principally in the spring.

Richland Creek. The green sunfish was too scarce in Richland Creek to obtain adequate numbers for positive judgment concerning their movement behavior, but the available information suggests that they moved very little. In 1948, 6 of 8 recaptures were in the same area where they had been marked 42 days previously. In another Richland Creek experiment to be described later, 10 of 11 recaptures remained at home during the summer. This behavior parallels that of the rock bass and longear sunfish very closely, and the tendency for the green sunfish to remain in a restricted area appears to be real. The principal restriction that should be placed on the conclusion is that the observations were conducted over a one-summer period and cannot be regarded as a year-to-year phenomenon as can that of the longear sunfish and rock bass.

Stott's Creek. No conclusion can be reached regarding the behavior of the green sunfish in Stott's Creek since only 2 of 20 marked there were recaptured. One of these was found at the place of original discovery and the other had moved one section away from its original point of capture.

Species with a larger home range

Smallmouth bass (*Micropterus dolomieu*)

Individuals of this sport fish weighing two pounds were caught in Richland Creek, but they reach greater size elsewhere. The smallmouth bass is more abundant in larger streams with a fast flow of water. It builds nests and spawns principally in the spring. In contrast to the insect larvae, small snails and the like that longear and green sunfishes feed upon, the mature smallmouth bass feed upon larger animals, such as other fishes and crayfish.

Richland Creek. The marked fish used to judge the movement of smallmouth bass ranged in size from 106 to 305 mm fork length and averaged 179 mm. A tabulation of the recaptures similar to that for the longear sunfish and rock bass indicated that they were not moving at random in the experimental area ($\chi^2 = 27.11$ with 12 d. f.), but the pattern of distribution was distinctly different. Of 11 recaptures which had been originally marked in sections A and B, 5 were found in their home section and 6 had strayed. In sections E and F, 5 of 8 recaptures had remained in section E where they were originally marked and 3 had strayed to another section. The smallmouth bass obviously did not confine their activities to areas as small as the other sunfishes. However, all species need not have home ranges of the same size. Even the smaller sunfishes may not all have home ranges of the same size, but under the conditions of the experiment it was only possible to demonstrate its presence or absence in a distance of 100–200 feet.

Since the stream was divided into two pool areas separated by a long riffle, it is possible to reclassify the data; the two sections A and B can be combined to form the downstream pool (now called

TABLE VI. *Number of smallmouth bass recaptured in Richland Creek during four years*

	Population percentage	Area of recapture	
		Area I	Area II
Area I Fish marked LP and RP	65.1	11	0
Area II Fish marked LV and RV	34.9	2	6

$\chi^2 = 11.5$ with 2 d.f., $p = <.01$.

area I), and the two sections E and F can be combined to form the upstream pool (now called area II). The marks LP and RP represent area I and the marks LV and RV represent area II. Analysis of the data based on this reclassification demonstrates that only 2 of 19 recaptures crossed the long riffle (Table VI). There is little chance that this pattern of distribution could be accounted for by fish moving at random after their release. This suggests that the smallmouth bass has a home range about twice as great as the other sunfishes under the conditions of this experiment. This is not a completely unexpected result because larger and more predatory animals generally have greater home ranges than smaller and less predaceous ones.

Stott's Creek. Twenty-one smallmouth bass were marked in Stott's Creek and 7 were recaptured. All 7 of the recaptures were made at the place where they were marked. Data from adjacent sections were not combined as they were in Richland Creek. Smallmouth bass, therefore, exhibit home ranges in at least two creeks and the phenomenon may be more widespread.

Spotted bass (*Micropterus punctulatus*)

The habits of the spotted bass are similar to the smallmouth bass. Generally speaking, the spotted bass does not become as large as the smallmouth bass, but in this study the average size was about the same.

Richland Creek. The size range of the marked spotted bass was 102–270 mm fork length and the average length was 161 mm. The remarks regarding the movement of smallmouth bass apply to this species as well. Only 1 of 16 recaptures moved across the long riffle (Table VII). This pattern of movement would not be expected on the basis of random distribution of the marked fish after their release. It is concluded that the spotted bass, like the smallmouth, has a home range about twice as great as that of the smaller sunfishes.

Stott's Creek. No spotted bass were found in Stott's Creek.

Golden redhorse (*Moxostoma erythrurum*)

The golden redhorse was the most abundant sucker in Richland Creek, and it is a common species in the smaller streams of the mid-west. It can easily be confused with other redhorse species, so each specimen was identified carefully. The golden redhorse feeds on bottom organisms. In the spring it spawns on riffles by depositing eggs in small depressions which are untended.

Richland Creek. The movement of golden redhorse resembled the behavior of the previous two species. Eighty-nine marked fish averaged 181 mm fork length with a range of 92 mm to 322 mm. Only 4 of 28 recaptures moved across the long

TABLE VII. *Number of spotted bass recaptured in Richland Creek during four years*

	Population percentage	Area of recapture	
		Area I	Area II
Area I Fish marked LP and RP	70.2	10	0
Area II Fish marked LV and RV	29.8	1	5

$\chi^2 = 12.41$ with 2 d.f., $p = <.01$.

TABLE VIII. *Number of golden redhorse recaptured in Richland Creek during four years*

	Population percentage	Area of recapture	
		Area I	Area II
Area I Fish marked LP and RP	53.7	15	2
Area II Fish marked LV and RV	46.3	2	9

$\chi^2 = 13.72$ with 2 d.f., $p = <.01$.

riffle in four years, (Table VIII), which is significantly different from the distribution to be expected on the assumption of random movement ($\chi^2 = 13.72$ with 2 d. f.). It is concluded that golden redhorse confine their movements to an area of about 300–400 feet in this stream.

It was a surprise to find that golden redhorse moved about so little. These fish ascend tributary streams to spawn in the spring and may move far. Richland Creek has no permanent tributaries within a few miles of the sampling site, and the spawning activities of this species are probably limited to the main stream itself.

Stott's Creek. Twelve golden redhorse were marked in Stott's Creek, and one was recaptured in the region where it was originally released.

Hog sucker (*Hypentelium nigricans*)

The hog sucker is common in small streams where it usually lives in the riffles or at the heads of pools. The writer is aware of no migratory movement of these fish coincident with spawning activities. In the flowing water of gravel streams the hog sucker deposits eggs in shallow cup-like depressions where they are left untended.

Richland Creek. Forty-one marked fish averaged 160 mm fork length and ranged from 140 to 204 mm. Most of the hog suckers were caught just below the riffle areas at the upper end of sections B and F. Of the 14 recaptures, 11 had remained in one or the other of the main pool areas where they had been marked and the other 3 had crossed the long riffle. A χ^2 value of 15.34 with 2 d. f. indicates a significant departure from random movement. The size of the home range is similar to that of the golden redhorse.

Stott's Creek. In Stott's Creek, where the species is more abundant, 196 hog suckers were marked and 73 were recaptured a month later. Most of these fish were small; they ranged from 80–235 mm fork length and averaged 104 mm. Sixty-six of the 73 recaptures (90.4 per cent) were found at the point of original capture. This indicates a strong tendency to remain at home and reinforces the impression obtained from the Richland Creek fish. Comparison between the creeks is done with some hesitancy because the fish did not represent the same size groups, but the conclusion that hog suckers have a home range seems to be substantiated.

EXPERIMENT II—MOVEMENT OF A SELECT GROUP FOR FOUR YEARS

Design of Experiment II

It became increasingly important to learn how long the fish occupied the same home range. The 1948 data for Richland Creek and the 1949 data for Stott's Creek showed that the majority of these fishes occupy a home range for a one-summer period. The 1949 and 1950 samples from Richland Creek showed the same tendency from one year to the next. The 1951 sample was taken two years after the last marking had been done, and this sample had the same characteristics as the others. According to this information, a majority of the fish occupied the same home range for two and possibly three years (some of the 1951 recaptures could have been derived from 1948 marking).

A method of re-marking the fish was devised whereby the movement of groups could be interpreted for more than two years. In 1949 the recaptures (derived

from 1948 marked fish) were fin-clipped in a fashion so that the section where they had originally been marked in 1948 could be recognized as well as whether they were home fish or stray fish. This required the removal of two more fins; only the pectoral and ventral fins were used. Recaptures of these "double-marks" were available in 1950 and 1951. It was possible to follow the movement of some individuals during most of their lifetime in this way. Only rarely do longear sunfish, rock bass or green sunfish reach age VI, and the smallmouth and spotted bass in Richland Creek were no older. The chance of catching these double-marks was small, and it was realized that the numbers of recaptures would hardly give a conclusive demonstration whether or not fish live in one place over a long period of time. However, the tendencies are for the most part clear-cut and the data may offer suggestions to others who are interested in the problem.

None of these double-marked fish were included in the data of Experiment I.

Results of Experiment II

1950 recaptures of double-marked fish. Four longear sunfish, 4 smallmouth bass, 1 golden redhorse and 1 hog sucker were recaptured which had been originally marked in 1948 and re-marked in 1949. One of the longear sunfish was found in section B in 1948, again in 1949 and again in the same place in 1950. Two longear sunfish were caught in section E in all three years. One longear was caught in section B in 1948, had moved to the adjacent section A in 1949 but was back in section B in 1950. It had confined its activity to the downstream pool area. Three of the four longear sunfish recaptured had remained in the same section for three years, and the other moved very little. No longears were caught which had moved across the long riffle.

Experiment I indicated that the majority of smallmouth bass confined their activity to one or the other of the two main pool areas and the same was true here. Three of the 4 smallmouth bass recaptures had remained in the same pool area for three years; the other had moved from the downstream pool across the riffle to the upstream pool.

The golden redhorse was found in the downstream pool in all three years and had confined its activity to section A.

The hog sucker was found in the upstream pool area for three years. It had remained in section F for two years and was located in section E in 1950.

Although the data are limited, there is nothing to disturb the conclusion that these species have a rather restricted home range. It can now be postulated that this behavior is characteristic over a three-year period.

1951 recapture of double-marked fish. Fifteen fish were caught in 1951 which had a double-mark: 8 longear sunfish, 2 rock bass, 4 smallmouth bass, and 1 hog sucker. Some of these recaptures could have been the same as were caught the previous year, but the extent to which this was true is unknown because individuals could not be recognized. Nothing is known about the activity of these fish in 1950; it is only known that they were marked in 1948, re-marked in 1949 and found again in 1951. The 1950 behavior might have been determined if they had again been re-marked in that year. However, further mutilation was not justified because the chance of recovery was very small.

Five of the 8 longear sunfish recaptures were discovered in the same section in 1951 where they were originally marked in 1948. Two sunfish which had occupied the same section in 1948 and 1949 had moved to an adjacent section in 1951. Only one longear had moved across the long riffle; it had moved from section E to B sometime between 1949 and 1951. All of these recaptures could be assigned to either age IV or V. Their average length was greater than the dou-

ble-marked recaptures of 1950; 1951 fish averaged 115 mm fork length and the 1950 fish averaged 102 mm.

One rock bass was found in section E in 1948, 1949 and 1951. This fish had probably remained within about 200 feet of the place where it was marked for four years. Another individual had moved from section E to F between 1948 and 1949, and it was found in section F in 1951. The movement of this rock bass suggests, as have the movements of other individuals, that an "old" home range may be abandoned and a "new" one adopted.

Smallmouth bass show a different pattern. Three of 4 fish had moved from the downstream pool across the long riffle to the upstream pool, while the other had remained in the same pool for four years. Possibly this species ranges over a wider area as it grows older.

The hog sucker was found in the same pool in 1948, 1949 and 1951.

The tendency to remain in restricted areas is not so pronounced among the 1951 recaptures. As fish grow older there seems to be a greater freedom of movement. Examination of the lengths of longear sunfish strays as compared to home fish of Experiment I suggests this same view (Table IX). In all four years the stray longear sunfish had a greater average length than the home fish. Other species showed this characteristic as well. There was considerable overlap in size among those that remained at home and those that strayed, but on the average it appears that the larger fish have the greater tendency to stray. Allen (1951) found that older brown trout travelled more freely than younger fish. Either the older fish have a larger home range or they may have a greater tendency to shift from one home range to another.

TABLE IX. *A comparison of the average fork length of longear sunfish classified as "home" and "stray" in Richland Creek*

	1948 mm	1949 mm	1950 mm	1951 mm
Home fish	86	99	106	110
Stray fish	104	103	111	113

EXPERIMENT III—A TEST OF THE TERRITORY HYPOTHESIS

Design of Experiment III

The home range phenomenon is not inalterably bound to territoriality, since aggressive behavior is not necessarily involved, but territoriality is suspected when evidence for home range is convincing. An experiment was designed to determine whether the fishes of Richland Creek maintain territories.

Provisionally accepting the hypothesis that territoriality is a real phenomenon among at least some of the species, the fish population was imagined as being under a constant state of tension. Competition for territories would create aggressive situations among the members of the population. Some fish would be eliminated or be buffetted about from place to place under such conditions. It might also be imagined that the weaker members of the population become the strays. However, as Greenberg (1947) found for immature green sunfish, the fish may have varying degrees of dominance, so that if one member was ousted from its territory it might compete successfully with a member close by. Large fish probably do not compete directly

TABLE X. *Fish marked in Richland Creek, 1951. Section B fish were transplanted to section E*

Species	Section A LP	Section B RP*	Section E LV	Section F RV	Total
Longear sunfish	53	55	63	36	207
Green sunfish	5	1	15	3	24
Rock bass	19	32	13	12	76
Smallmouth bass	4	3	4	1	12
Spotted bass	6	1	0	2	9
Golden redhorse	32	9	7	19	67
Hog sucker	0	19	7	21	47
Total	119	120	109	94	442

* 6 longear sunfish, 2 rock bass, and 1 hog sucker bearing the RP mark from a previous year were also transplanted. Stray fish found in section B were destroyed.

TABLE XI. *The distribution of marked longear sunfish in Richland Creek two weeks and six weeks after transplanting section B fish to section E*

Mark	Two weeks after transplanting				Six weeks after transplanting			
	Section A	Section B	Section E	Section F	Section A	Section B	Section E	Section F
LP	15	4	0	0	9	8	0	0
RP*	0	26	6	3	0	18	4	7
LV	0	0	37	2	0	1	23	9
RV	0	0	5	11	0	0	2	14

* Had been transplanted to section E.

with small ones at any given time because they usually occupy different niches. In Richland Creek, as is usual, the small fish live in shallow water and the large ones in pools. Some time during their lifetime the younger, faster-growing fish must enter deeper water and compete with larger fish, of the same or other species. These illustrations by no means exhaust the possible variety of phenomena associated with territoriality.

Assuming that territoriality may be a true behavior pattern among some or all the species considered here, at least 3 postulates may be made. (1) Fish move rapidly into an underpopulated area. (2) A "foreign" population, on suddenly entering a well-established population, competes with the others, but the residents have some advantage in the competition, as Braddock (1949) has shown for *Platypoecilus maculatus*. As a result the "foreign" fish move to a greater extent than the others. (3) The well-established individuals move more than they usually do as a result of the competition. If these hypotheses could be satisfied by experiment, then evidence regarding territoriality would be more convincing.

The physical features of Richland Creek were ideal for an experiment to test the territorial hypotheses. Section B was underpopulated by removing all fish of all species that could be caught. The section B fish were placed in section E immediately after they were weighed, measured, and marked in the usual way. Section E thus became overpopulated. Before section B fish were transplanted, all other sections had been traversed and the fish marked in the typical manner (Table X).

The small residual population of marked fish in the stream presented little difficulty in the interpretation of the data because most of them were home fish. The whole experimental area was traversed twice after the fish were transplanted in order to follow their movement, once two weeks after transplanting and again six weeks after transplanting. No high water or other unusual circumstance occurred between the time the fish were marked and their subsequent recapture.

The success of the experiment hinged on the assumption that the size of the population in all sections prior to the transplantation was near or at its maximum. This assumption seems to be reasonable since no drastic changes in the abundance of individual species or in the species composition were evident during the four years.

Results of Experiment III

Longear sunfish. The most striking feature of the transplantation experiment is that a majority of the longears, which had been transferred to section E, moved downstream over the long riffle to their original home (Table XI). This movement indicated that the riffle was a behavioral rather than a mechanical barrier. Twenty-six of 35 RP recaptures were taken in section B two weeks after transplanting, 18 of 29 recoveries in the six-week sample. A χ^2 test of independence

indicated that there was no significant difference between these samples ($\chi^2 = 0.575$ with 1 d. f.). Thus, the entire movement could be accounted for within two weeks after the fish were transplanted. This movement agrees with hypothesis 2, above.

The migration back to the original point of capture could also be interpreted as "homing," a well-known phenomenon among some anadromous fishes like the salmon. Until recently such behavior had never been described for non-migratory fishes. Larimore (1952) has performed some homing experiments with smallmouth bass and longear sunfish by following the movement of individuals after transferring them from their home pool to other parts of a stream. He cites strong evidence that smallmouth bass show homing behavior. In the light of this evidence, the homing interpretation cannot be eliminated. However, Larrimore's experiments did not conclusively demonstrate a tendency for longear sunfish, the species under discussion here, to return to their home pool after being transferred to a new location. Therefore, the movement in our experiment will be interpreted as a result of competition between "foreign" and well-established individuals.

The redistribution of the transplanted longears that remained above the riffle was interesting, since 6 of 9 recaptures (67 per cent) were found in section E two weeks after they were transplanted, but only 4 of 11 (36 per cent) were in section E six weeks after transplanting. Though the sample was smaller than desirable, the results suggest that increased competition led to increased movement of the transplanted longears out of the area.

In the two-week sample of section E fish, 37 of 39 were found at home. Of 33 fish in the six-week sample, 23 were at home. A chi-square comparison of these data indicates that the difference between the samples is significant ($\chi^2 = 6.44$, with 1 d. f., $p = .012$). Some of the longears which were well-established in the area moved away after it became overpopulated (see hypothesis 3 above).

Five of 16 longears originally marked in section F were strays into section E in the two-week sample, but only 2 of 16 were present in section E in the six-week sample. This could have been the result of chance ($\chi^2 = 0.732$ with 1-d. f.), but the migration away from the overpopulated area agrees with the trends already reported.

A progressive movement into the underpopulated area (section B) from section A seems to have taken place, as would be expected if the first hypothesis were true. Four of 19 longears (LP) had strayed into the underpopulated area two weeks after the fish had been removed and 8 of 17 were strays into section B in the six-week sample. This movement is also in accord with expectation.

The tentative conclusion is offered that territory competition was the cause of the movement, but it is tempered with the knowledge that it is based on fewer recaptures than desirable and also that it is not based on direct observation of such competition. The expected movements were all confirmed, however, and there would be little chance that they were the result of random movement.

Rock bass. The movement of 32 transplanted rock bass, and the movement of the well-established fish were similar to that of the longear in most respects (Table XII). Two differences were noticed: (1) the majority of the rock bass stayed above the long riffle after transplanting and (2) the fish from section A (LP) did not show a progressive movement into the underpopulated section. So few LP recaptures were made that sampling error could account for the difference between the two samples, although the data may reflect the actual movement that occurred. The fact that some rock bass moved back across the long riffle in such a short time again proved that the riffle was not a mechan-

TABLE XII. *The distribution of marked rock bass in Richland Creek two weeks and six weeks after transplanting section B fish to section E*

Mark	Two weeks after transplanting				Six weeks after transplanting			
	Section A	Section B	Section E	Section F	Section A	Section B	Section E	Section F
LP	**7**	2	1	1	**4**	0	0	0
RP*	0	**3**	4	2	1	**2**	6	6
LV	0	0	**5**	1	0	0	**2**	4
RV	0	0	1	**3**	0	0	0	**5**

* Had been transplanted to section E.

ical barrier to fish movement. The pattern of movement resembled that of the longear and it is tempting to interpret the limited data by the same hypothesis, *i.e.* the movement was caused by a competition for territories.

Other species. The information about the green sunfish, smallmouth bass, spotted bass, golden redhorse, and hog sucker was not sufficient to interpret their movement in the light of the territory hypothesis.

DISCUSSION

If the data have been interpreted correctly from the point of view of home range and territory, some new light is thrown on the general characteristics of fish populations in small streams. In streams with riffle-pool development, such as Richland Creek and Stott's Creek, each pool can be considered as a more or less isolated unit containing a natural population of its own. The chances are great that once a fish becomes established in an area it will remain there for most, if not all, of its lifetime. This sounds much like the statement by Burt (1940) concerning the wood mouse (*Peromyscus leucopus*): "Once a mouse settles down and establishes a territory, it usually, but not always, remains there for life." The tendency for fish to remain in familiar surroundings may be a more common characteristic than is generally realized. It is interesting in this connection to read Fraser-Brunner's (1950) statement that for six months he observed a butterfly fish (*Chaetodon melapterus*), identifiable by a scarred fin, in the same position near a rock. Scott (1949) found that rock bass in the Tippecanoe River in Indiana moved very little from year to year. Shuck (1943) found this true for brook trout (*Salvelinus fontinalis*), Shetter (1937) described a similar situation for brown trout (*Salmo trutta*), and Larimore (1952) has shown that smallmouth bass are associated with "home pools." It appears that the fish population of a small stream may be thought of as a series of discrete, natural units rather than as a single, homogeneous, freely-mixing group. The natural intraspecific and interspecific changes in a fish population in one part of a stream may bear no relation to events occurring in another part of the stream.

Since this paper was written, Allen's (1951) work on the Horokiwi Stream of New Zealand has come to hand and some of his results are strikingly similar to ours. In a situation quite comparable with ours, 42 recaptures of brown trout were made and all but 2 were found where they were tagged. Allen regards the trout population of the Horokiwi as being not only isolated and self-contained, but also composed of a succession of distinct local populations. This is borne out further by his discovery that the trout had different growth rates in different parts of the stream.

Home range and territory have not been satisfactorily distinguished by the experimental procedure. They may or may not be independent of one another. The purely arbitrary selection of a boun-

dary between sections A and B and between sections E and F make it impossible to calculate the actual size of the home range. It is conceivable that a determination of this sort might be made by studying sections of progressively smaller size. If the home range concept is valid, a section size would finally be reached where the tendency to stay in one place would no longer be evident. In effect this is what was described in Richland Creek where the majority of longear sunfish and rock bass were found to remain within the 100–200 foot sections, while the larger species showed no tendency to remain in such small areas. When the boundaries were increased, the home range of the larger species was revealed.

The territory seems to be a much more satisfactory way of thinking about the interaction between members of a population than the home range. Territory stresses the type of competition which seems to have been developed in the overpopulated area of Experiment III. It is gratifying to get direct evidence for the territory concept among fishes from Greenberg's (1947) laboratory experiments with immature green sunfish. In his excellent paper he states: "Even under our laboratory conditions, with oversimplification of habitat and limitations of space, territoriality is an outstanding phenomenon in the social life of immature sunfish." Greenberg also proves that green sunfish have social rank built up much like the peck-order of chickens. Braddock (1945) shows that *Platypoecilus maculatus* has a social order although it does not have territories. Noble and Curtis (1939) described the social behavior in the jewel fish (*Hemichromis bimaculatus*) which has reproductive territories. Concepts of territory and social rank lead to the consideration that the amount of food and the number of young produced by fish are not the only limitations placed on natural populations. The natural aggressive action of fish toward one another also limits the population size.

Greenberg and others have observed that as a general rule larger fish dominate smaller fish. If this is the case, the smaller fish would become the strays of our experiments. However, it was shown that in Richland Creek the larger fish of a given species wandered more than smaller ones. This discrepancy might be explained by the limitations of the aquarium experiments. Greenberg used only small fish of about the same size within the confines of small aquaria. Fish of all sizes are living together in the same general area in nature. In a rapidly growing population, the young fish which are being recruited into the older group will sooner or later be thrown into direct competition with the older fish. The younger fish might then have the advantage of youth and be able to dominate an older one and force him to seek territory elsewhere.

The importance of the stray fish should not be overlooked. Here is a reserve supply which is available to occupy territories left vacant for one reason or another. They become the elements which can move and repopulate decimated areas. They may also be important in the distribution of the species over the geographic limits of tolerance.

Intense competition such as pictured here does not lead to chaos in a population but rather forms the structure for stability among members of a group. Greenberg's aquarium fish usually retained a stable relationship with one another after the hierarchy and territories had become established. Once a fish learned his place in the group he was usually content, or forced, to remain there. Greenberg says, "Territories are stable but may undergo changes such as elimination of one, transfer of ownership, shifts in position and boundaries, and variations in relative aggressiveness of the possessors."

The tendency for fish to stay within circumscribed limits may not be limited

to streams. There is some evidence that certain species show the same behavior in lakes. A few examples can be cited where the information is clear. Lagler and Ricker (1942) studied the fish populations of Foots Pond in Indiana (47.5 acres). They found that the fish in the south end of the pond did not mix freely with those in the north end. They stated: "Of 67 marked white crappies (*Pomoxis annularis*) recaptured in the southern part of the pond . . ., only 4 had moved in from the north; and only 3 of 22 retaken in the northern part had come from the south." These fish were not moving randomly in the pond. Omand (1951), who netted three Canadian lakes intensively, found that the nets fished well for a few days and then the catches dropped off. Good catches could be made if the nets were moved only a short distance (200 yards). Omand says, "The entire impression was one of exploitation of a series of local populations, usually in sheltered bays." Worthington (1950) noticed a similar phenomenon while fishing intensively for perch in Lake Windemere. It is a custom in studies of fish populations in Indiana lakes to move traps each day or two in order to avoid such occurrences, because circumstances similar to Omand's have been noticed often.

Ball (1947) tagged several species in Third Sister Lake, Michigan (10 acres). Eighteen of 27 bluegill (*Lepomis macrochirus*) recaptures had moved no more than 65 yards from their point of original capture and 12 were reported not to have moved at all. Yellow bullheads (*Ameiurus natalis*) showed the same tendency; 19 of 27 had moved no more than 100 yards from where they were marked and 11 had not moved at all. He reported that largemouth bass (*Micropterus salmoides*) showed no tendency to remain in one location. Shoemaker (1952) described an experiment in a 90-acre lake in which pumpkinseeds (*Lepomis gibbosus*) and yellow bullheads had affinity for definite areas in the lake. This experiment also provided some evidence that these species have homing behavior. Rodeheffer (1941) fin-clipped and tagged many fish of various species in Douglas Lake, Michigan, during several years of investigation. The movement of his fish was restricted. One of his most interesting statements in this connection is: "It is most striking that not a single fish of the 4,557 marked at Grapevine Point from 1937 to 1939 were recovered at any other point in the lake." Sportsmen and collectors from the University of Michigan Biological Station were active in all these years and had been informed about the marked fish.

Other examples could be brought forward to support the fact that some lake species move very little. The fact itself is important, but when interpreted with regard to the social habits of fishes, it acquires even greater meaning, for now some insight is obtained as to why such behavior might be expected to occur.

The practical application of the social habits of fishes has received very little attention. Langlois (1936) used such information in his program of rearing smallmouth bass in ponds, but this is the only case of which the writer is aware. The lack of success in stocking fish in streams and lakes with either fingerlings or larger fish may in part be due to the intense competition in an already "saturated" environment. The social habits of fish deserve more attention in the future as the reward seems promising.

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Summary

Investigation of the factors influencing fish populations has centered on food, feeding habits, reproductive behavior, reproductive potential, growth, and mortality. These factors have been studied from the viewpoint of the population as an aggregate of animals. The present work on the fish populations of two streams attempts to investigate the competitive interaction between individuals as another factor affecting the size and structure of the group.

The information concerning the movement of fishes in a bedrock stream and a gravel stream was interpreted with respect to home range and territory, phenomena best known among mammals and birds. Experimental areas in each stream were subdivided into four sections and the fish of each section were marked distinctively by fin-clipping. The movements of the fish in the bedrock stream were traced for four years. The gravel stream was studied for one summer.

Longear sunfish, rock bass and green sunfish moved about very little in the stream from one year to the next and some of them remained in one stream section for as long as four years, which is near their life-span. The size of the home range of these small sunfish in the stream could be estimated at 100–200 feet under the conditions of our experiment. The movement of the smallmouth bass, spotted bass, golden redhorse and hog suckers was greater than the sunfishes. These species had home ranges of about 200–400 feet in the stream.

All of the species respected the stream riffles as boundaries. It is concluded that the fish population of a small stream with riffle-pool development may be considered as a series of discrete, natural units rather than a single homogeneous, freely-mixing group.

The concept of competitive territories develops logically from a convincing demonstration of home range. Aggressive behavior of the fish in the streams could not be observed, so an experiment was designed to test the hypothesis that fish have territories. Separate sections in an experimental area were underpopulated and overpopulated. The movements of longear sunfish and rock bass under these circumstances suggested that the territory hypothesis may be true. Aggressive behavior among individuals of a fish population may be one of the factors determining the characteristics of fish populations.

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THE BEECH GAPS OF THE GREAT SMOKY MOUNTAINS

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INTRODUCTION

The beech gaps are one of several striking vegetation types of higher altitudes in the Great Smoky Mountains of Tennessee and North Carolina. The term "beech gap"[1] refers to relatively high (above 5,000 feet elevation) forests of beech (*Fagus grandifolia*[2]), which usually are found on the south-facing slopes of local dips in east-west or northeast-southwest ridges. Their boundaries are very sharply marked. The dominant forest type at elevations greater than about 5,000 feet in the Great Smokies is spruce-fir (*Picea rubens-Abies fraseri*). The beech forests occur as small stands or deciduous "islands" in this forest (Fig. 1). Present over considerable areas also are successional burn forests, composed of a variety of young trees. These occur generally where spruce-fir or spruce had previously stood.

The area covered by high elevation beech forest is quite small. Ashe (1922) stated that in North Carolina it was "doubtful if the aggregate area exceeds 10,000 acres." The total acreage in Tennessee is in all probability less. Some of the areas that formerly supported beech forests have been cleared in historic times. Cain (1937) cites as examples Newfound Gap and Indian Gap, the two lowest and widest passes through Forney Ridge between Knoxville, Tennessee, and Asheville, North Carolina. Some beech still exists at Newfound Gap, but the beech forest is now completely absent from Indian Gap.

In 1947 and 1948, studies were made by the present author of a number of beech gaps occurring principally along Forney Ridge, a high mountain ridge running roughly from Charlie's Bunion westward through Newfound Gap to Clingman's Dome, in the central part of the Great Smoky Mountains National Park. The Appalachian Trail runs along the top of Forney Ridge. A total of 13 small beech forests, occurring in dips or "gaps" of the ridge, were studied. In addition, a large beech gap, locally known as Trillium Gap or Grassy Gap and situated in a pass between Mt. LeConte and Brushy Mountain, was studied. In all cases, except that of the Double Springs beech forest (west of Clingman's Dome), and Trillium Gap, the forests were surrounded by virgin spruce-fir forest. The large beech forest at Double Springs Beech Gap was bordered at lower altitudes by the lowland cove forest, and in a few other instances the beeches came into contact with hemlocks at their lower limits. Trillium Gap was bordered on the north by spruce-fir, on the south by a heath bald (Cain 1931), on the east by a lowland beech-hemlock forest, and on the west by a forest dominated by yellow birch (*Betula lutea*). The beech forests were also considered virgin and climax for their site. In addition to the phytosociological studies, reported below, microclimatic studies were attempted, but had to be discontinued after a short time due to depredation by black bears. Atomometers and maximum-minimum thermometers were set up in several of the beech gaps but were demolished by bears in a few days time.

PHYTOSOCIOLOGICAL STUDIES

Species lists were prepared for 14 of the beech gaps. Two other beech gaps were noted along Forney Ridge but were very small, less than a quarter acre in area, and were not studied. In Table I,

[1] The forests also have been called "beech orchards" locally.

[2] With respect to taxonomic nomenclature, Fernald (1950) was followed where applicable and Small (1933) in the remainder of cases.

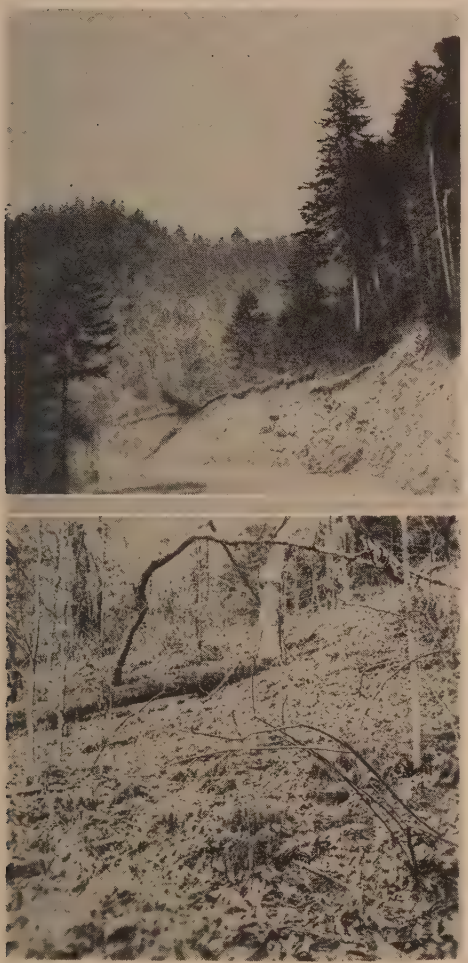

FIG. 1. Upper. One of the beech gaps studied; located about two miles southwest of Newfound Gap, along Forney Ridge. Lower. Interior of the beech forest. Photographs by Hugo H. Iltis.

species present in 21% or more of the 14 stands are listed, and in addition the presence data are summarized. It will be noted that only one species was present in all 14 of the stands, *Fagus grandifolia*. None of the other 6 species found in over 80% of the stands could be considered strictly characteristic of the beech forests. Many of the species were found also in either the spruce-fir or burn forests, and a few were more characteristic of the rich mixed mesophytic cove forests of lower elevations. Beech, itself, is one of the dominants of the cove forests. However, recent research by Camp (1940, 1950,

TABLE I. *Presence of species in 14 individual beech stands*

	Number	Per cent
1–20% of stands	62	56
21–40%	20	16
41–60%	7	6
61–80%	15	14
81–100%	7	6
Totals	111	100

Species with presence of 21% or better:	Presence
Fagus grandifolia	100%
Laportea canadensis	93
Poa alsodes	93
Rubus canadensis	93
Athyrium filix-foemina var. *michauxii*	86
Carex debilis var. *rudgei*	86
Picea rubens	86
Carex artitecta	79
Stellaria pubera var. *sylvatica*	79
Trillium erectum and var. *album*	79
Angelica triquinata	72
Luzula bulbosa	72
Prenanthes sp.	72
Senecio rugelii	72
Aster spp.	64
Carex intumescens var. *fernaldi*	64
Houstonia serpyllifolia	64
Smilax herbacea	64
Solidago glomeratus	64
Viburnum alnifolium	64
Viola pallens	64
Betula lutea	57
Aesculus octandra	50
Clintonia borealis	50
Dryopteris spinulosa var. *americana*	50
Amelanchier laevis	43
Claytonia virginica f. *micropetala*	43
Lilium superbum	43
Abies fraseri	36
Hydrophyllum virginianum	36
Oxalis montana	36
Polygonatum pubescens	36
Tiarella cordifolia	36
Boehmeria (?)	29
Erythronium americanum	29
Eupatorium rugosum	29
Impatiens pallida	29
Prunus serotina	29
Rumex crispus (?)	29
Smilacina racemosa	29
Thalictrum dioicum	29
Acer pennsylvanicum	21
Acer rubrum	21
Cuscuta sp.	21
Eupatorium sp.	21
Veronica officinalis	21
Viola sp.	21

1951, Braun 1950) indicates that the beech of the upper gap forests and the beech of lowland forests are quite different genetically. Camp recognizes three distinct genetic "types" of beech in eastern North America, the *white beech,* ". . . found mainly at low elevations in southeastern and southern states . . .," the *red beech,* ". . . characteristically found on the well-drained slopes of the Southern Appalachians . . .," and the *gray beech,* which ". . . occurs at the higher elevations in the Southern Appalachians (being found only above 4,500 feet in the Great Smoky Mountains and southern Blue Ridge, often within the red spruce zone) . . ." and ". . . reappears in pure stands above 2,000 feet elevation in the Adirondack Mountains of New York, at expected elevations in Vermont, New Hampshire, and Maine, and comes to sea level in appropriate habitats from central Nova Scotia to Cape Breton Island; westward, in a narrow band, it follows the lower border of the northern coniferous forest to the limits of the beech in the Great Lakes region" (Camp 1950).

The genetic difference between the red and gray beeches is illustrated in the central part of the Smokies by the fact that beech does not occur in any form between the altitudes of about 3,500 feet and 4,500 feet. A situation similar to this has been observed in the Cumberland Mountains of eastern Kentucky, where beech does not occur between 2000 and 4000 feet (Braun 1950).

Short species lists, doubtless incomplete, for the spruce-fir and burn forests along Forney Ridge, are presented below, for purposes of emphasizing the overlap of species.

A total of 13 sample plots were run in 4 of the beech gaps. Twelve of these were

Flora of burn forests

Trees	Shrubs
Abies fraseri	*Diervilla sessilifolia*
Betula lutea	*Menziesia pilosa*
Picea rubens	*Ribes* sp.
Prunus serotina	*Rubus canadensis*
Pyrus americana	*Sambucus pubens*
	Vaccinium erythrocarpum
	Viburnum alnifolium

Herbs	
Angelica triquinata	*Lilium superbum*
Aster sp.	*Monarda didyma*
Carex debilis var. *rudgei*	*Phleum pratense*
Carex intumescens var. *fernaldii*	*Poa pratense*
Carex spp.	*Poa alsodes*
Chelone lyoni	*Rudbeckia laciniata*
Cuscuta sp.	*Rumex acetosella*
Danthonia sp.	*Senecio rugelii*
Eupatorium sp.	*Solidago glomerata*
Houstonia serpyllifolia	*Stachys* sp.
Hypericum mitchellianum	*Thalictrum* sp.
Impatiens pallida	*Tarutvetteria caroliniensis*
Festuca obtusa	*Trifolium repens*
	Veratrum viride

Flora of spruce-fir forests

Trees

Abies fraseri
Acer pennsylvanicum
Acer spicatum
Amelanchier laevis
Betula lutea
Fagus grandifolia
Picea rubens
Prunus serotina
Pyrus americana

Shrubs

Ilex montana
Rhododendron catawbiense
Rubus canadensis
Sambucus pubens
Vaccinium corymbosum var. *glabrum*
Vaccinium erythrocarpum
Viburnum alnifolium

Herbs

Angelica curtisii
Aster acuminatus
Athyrium filix-foemina var. *michauxii*
Chelone lyoni
Clintonia borealis
Disporum lanuginosum
Dryopteris marginalis
Dryopteris spinulosa var. *americana*
Lycopodium lucidulum
Monotropa uniflora
Oxalis montana
Polypodium virginianum (?)
Senecio rugelii
Solidago glomeratus
Streptopus roseus

run in 3 gaps and were each 10 meters on a side. A single sample plot, 10 × 30 meters, was run in the fourth gap. Only the arborescent stratum was sampled. The sampling data are presented in Table II. The overwhelming dominance of beech is apparent in total numbers of stems, distribution, basal area, and coverage. A feature of the beech forests is the height of the canopy. Only rarely was a beech seen that exceeded 50 feet in height, and in general the canopy was about 30 feet high. An occasional buckeye (*Aesculus octandra*) or spruce (*Picea rubens*) would stand above this. The beech trees were for the most part small, bent, and twisted. Self-pruning had not occurred, and this, added to the steepness

TABLE II. *Averaged data for all beech stands sampled (arborescent stratum)*

Species	Frequency[1]	Number of trees less than 1″ DBH	Per cent	Number of trees more than 1″ DBH	Per cent	Basal area	Per cent basal area	Basal area per acre	Number size classes[2]	Average coverage class[3]
Fagus grandifolia	100%	187	91.1	96	72.8	37.13	62	99.123	3	3
Aesculus octandra	61	8	4.0	13	9.8	6.1	10	16.267	3	1
Acer saccharum	31	1	0.5	5	3.8	6.63	11	17.702	3	1
Picea rubens	31	1	0.5	12	9.1	4.41	7	11.775	3	x
Betula lutea	54	5	2.4	5	3.8	5.87	10	15.775	3	1
Abies fraseri	8	1	0.5	0					1	x
Amelanchier laevis	8	1	0.5	0					1	x
Pyrus americana	8	1	0.5	0					1	x
Prunus serotina	8			1	0.7	0.09	0.1	0.24	1	x
Totals	100	205	100	132	100	60.225	100.1	160.78	3	

[1] Frequency for 13 sample plots, number of trees less than 1″ DBH for 1,200 sq. m., other data for 1,500 sq. m.
[2] Size classes—less than 1″ DBH, 1″–3″ DBH, more than 3″ DBH.
[3] Coverage classes—x—less than 1%; 1—1%–5%; 2—6%–25%; 3—26%–50%.

of the slopes on which the forest grew, made sampling work very difficult. Many broken branches, the result of past wind storms, lay on the ground.

As an indication of the distribution of size classes within these forests, data are presented in Table III from the analysis of the Double Springs Beech Gap. These demonstrate the proponderance of small- and medium-sized trees of beech and the scarcity of relatively large trees in the beech forests. These counts were made on an area 10 × 50 meters in extent. In spite of the small size of the larger beeches, it was felt that they were probably older than they appeared. Increment borings or stump counts were not made, however.

The type of reproduction in the gaps is not indicated by Table III. Reproduction seemed to be almost entirely vegetative, from suckers or root sprouts. Though a diligent search was made, not a single seedling or transgressive undoubtedly growing from seed was found. However, seed was produced by the larger trees in the gaps in 1948.

In Figure 2, phytographs are presented for the 9 species of trees sampled in all the plots. Here again the dominance of beech is apparent. This phytograph differs from the one proposed by Lutz (1930) and in general use. It is thought that the substitution of coverage percentage for frequency percentage on one of the axes increases the significance of the phytograph in portraying actual dominance in this instance. It will be noted that 4 of the tree species found occur only in a single size class and are unimportant in dominance categories.

The herbaceous flora of the beech gaps is quite varied, a total of 88 different species of herbs being noted during the spring and early summer of 1947 in the 14 beech forests studied. The herbaceous flora of a relatively large (about 4 acres) beech gap about 2 miles southwest of Newfound Gap (shown in Fig. 1) was sampled on May 11, 1947. The data (Table IV) indicate that, when sampled, 4 species were very abundant and widespread: *Claytonia virginica* forma *micropetala, Phacelia fimbriata, Aster* sp. (not identifiable), and *Erythronium americanum.* Earlier in the year, *Houstonia serpyllifolia* had been the most conspicuous herb; about two weeks after sampling *Phacelia fimbriata* was flowering and was most conspicuous. Summer and autumn aspects were not seen here. In some of the gaps, the sedges (*Carex* spp.) and *Poa alsodes* are much more important than here. Only a few adventive or weedy plants were found and all these occurred only along paths or roads through some of the gaps. Disturbance of the vegetation of the gaps studied, either by grazing animals or by man, seems to have been very small.

Life-forms (Raunkiaer 1934) were determined for 93 of the more abundant species of the beech gaps, and the percentages of plants in each of the five major life-form classes are given in Table

TABLE III. *Distribution of arborescent species into one inch DBH classes, Double Springs Beech Gap. Count made on an area 500 square meters in extent*

Species	Below[1] 1″	1″	2″	3″	4″	5″	6″	7″	8″	9″	10″	11″	12″	Total
Fagus grandifolia	96	3		7	19	35	24	12	2		2		1	201
Aesculus octandra	7		2		1	2	1				1	1	1	16
Abies fraseri	1													1
Pyrus americana	1													1
Amelanchier laevis	1													1
Totals	106	3	2	7	20	37	25	12	2		3	1	2	220

[1] Only trees above six feet high counted.

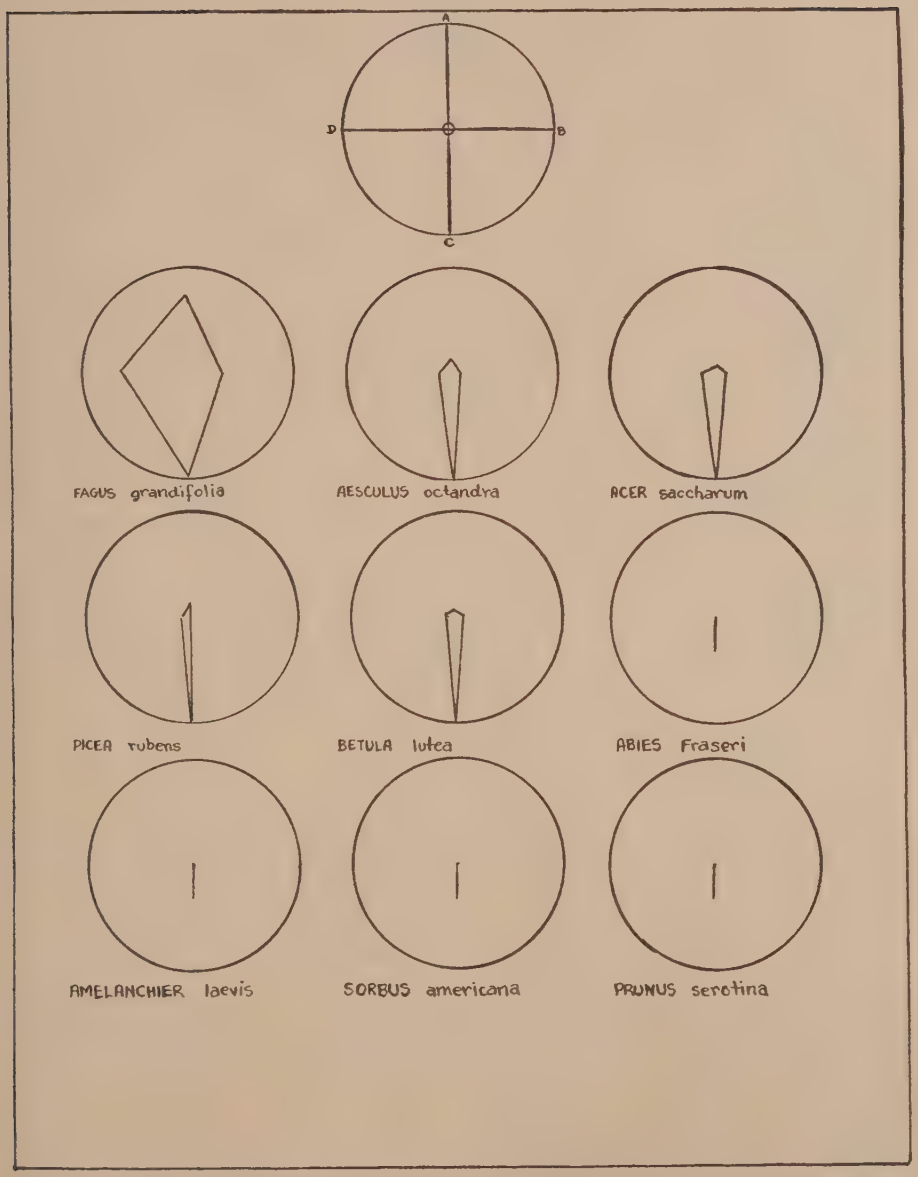

FIG. 2. Phytographs for all trees found in the four beech forests sampled. Data in Table IV. Key: O-A—density percentage; O-B—coverage class (percentage); O-C—number of size classes (percentage); O-D—basal area percentage.

V, together with Cain's data for the total flora of the Great Smoky Mountains National Park. The beech forests are distinguished principally by having higher percentages of phanerophytes (Ph), chamaephytes (Ch), and cryptophytes (Cr). The percentage of annuals (Th—therophytes) is much lower than that of the

TABLE IV. *Herbaceous flora, Forney Ridge Beech Gap No. 1, as sampled by 25 sample plots, 0.5 m × 2 m, May 11, 1947. Braun-Blanquet's abundance and coverage scales (1932) were used*

Species	Frequency	Abundance	Coverage	Periodicity
Claytonia virginica f. *micropetala*	100	3	2	flowering
Phacelia fimbriata	92	3	2	bud
Aster sp.	88	2	1	vegetative
Erythronium americanum	84	2	1	veg.
Stellaria pubera var. *sylvatica*	44	1	1	bud
Rudbeckia laciniata	32	1	1	veg.
Thaspium spp.	32	1	1	veg.
Houstonia serpyllifolia	28	1	1	flowering
Poa alsodes	24	1	1	flowering
Monarda didyma	24	1	1	veg.
Dentaria diphylla	24	1	1	veg.
Rubus canadensis	20	1	1	veg.
Dicentra cucullaria	16	1	1	veg.
Carex sp.	12	1	1	veg.
Thalictrum dioicum	12	1	1	veg.
Allium tricoccum	12	1	1	veg.
Trillium erectum	12	1	1	bud
Luzula bulbosa	8	1	1	flowering
Dryopteris spinulosa var. *americana*	8	1	1	veg.
Viola sp.	8	1	1	flowering
Carex artitecta	4	1	1	flowering
Lilium superbum	4	1	1	veg.
Senecio rugelii	4	1	1	veg.
Solidago glomeratus	4	1	1	veg.

Frequency Classes

I—13—54%
II— 6—25%
III— 1— 4%
IV— 0— 0%
V— 4—17%

park as a whole, which may be taken as indirect evidence of the climax nature of the beech forests.

CONCLUSIONS

The beech forests are characterized by both their location, in gaps or small dips in the ridges, and by their appearance. The tree stratum is dominated by small, gnarled, broken beech trees which occur very densely. The forest is more open in nature than either the spruce-fir forest or the burn forest, though the trees are closely spaced. Leaf mold is comparatively thin in the beech forests, though very thick in the adjacent spruce-fir. The pH of the soil varies from about 4.5 to 6.0 in the beech forests and from 3.6 to 3.8 in the spruce-fir (Cain 1931, 1937). The beech forests are well-developed only on south slopes, whereas the spruce-fir is found on all slopes. Shrubs and transgressive growth are much greater in the beech woods than in the spruce-fir. The herbaceous flora of the beech forests is relatively great compared either to the spruce-fir forests or the burn forests.

The occurrence of beech forests in the spruce-fir zone and at an altitude 1,000 feet above the nearest lowland beech forests is difficult to explain. Camp (1950) states that "There is considerable evidence that, at some time in the late Tertiary, the present three basic types of the beech population of eastern North America were quite distinct species." Since that time there has been considerable introgression among the three with consequent partial obliteration of morphological differences.

The microclimates of the beech forests and the spruce-fir forests are quite dif-

ferent as indicated both by observation and about four week's measurements of maximum and minimum temperatures in April, May, and June, 1947. Stations in the beech gap were found to have considerably greater extremes of temperature during the period of study. It is doubtful if rainfall is a factor of importance, due to the great amount (over 80 inches) which falls annually between Clingman's Dome and Newfound Gap. Burning does not seem to have been of importance. No evidence of it was noted in those gaps examined by the author.

Wind, in the opinion of the present author, may be an extremely important factor in the establishment and persistence of beech. Based on observation alone the force of the wind in the beech gaps seem always stronger than in adjacent forests. The wind seems to funnel through the gaps. "Air currents circulate through the gaps when everywhere else the air is quiet. . . . Through the season clouds drift back and forth through these gaps and in the winter the sleet storm are frequently severe" (Cain 1937). During the winter of 1946–47 there was one particularly bad windstorm in the mountains which felled many large trees in the spruce-fir forests. However, wind damage was far more severe in the beech gaps. In the beech gap where the microclimate studies were attempted it was almost impossible to walk for fallen trees and broken branches.

The soils of the beech gaps and spruce-fir forests are quite different. Cain (1937), discussing Trillium Gap, says that "In the gap the soil is relatively deep, friable, rich and well-drained, but not excessively so. Also the soil is only weakly acid and there is no accumulation of peat, excessive depth of litter, nor podzolization. A short distance away from the beech woods, in the spruce forest or in the heath bald, all these conditions are reversed. . . ."

It is impossible, without detailed study, to determine whether the various manifestations of the microclimates are the causes or results of the beech forests. Insolation, temperature, and soil differences may be the result of continuous occupancy of an area by a certain type of forest, rather than its original cause.

TABLE V. *Life-form spectra for beech forests and the total flora of the Great Smoky Mountains National Park*

Area	Number of species	Percentage of:				
		Ph	Ch	H	Cr	Th
Beech forests Great Smoky Mts. National Park (Cain 1945)	93	26	5	42	24	3
Normal (Raunkiaer 1934)	1142	19.5	1.7	52.1	15.1	11.5
	1000	49	9	26	6	13

SUMMARY

Phytosociological studies of almost pure beech forests occurring on the south-facing slopes of "gaps" or dips along Forney Ridge in the Great Smoky Mountains were made in 1947 and 1948. Accumulated data demonstrate the preponderance and sole dominance of beech (*Fagus grandifolia*). Floristic comparisons between the flora of the beech forests and the floras of adjacent spruce-fir (the altitudinal climax) and successional burn forests indicated that very few species might be considered characteristic of the beech forests.

The recent work of W. H. Camp on the genetic status of beech was discussed. The beech at higher elevations in the Southern Appalachian Mountains is the genetic type Camp designated as "gray beech." "Red beech" is a prominent member of the cove forests at lower elevations in the Southern Appalachians.

With regard to the persistence of the beech at high altitudes in the Smokies, it was concluded, after an analysis of environmental factors, that the ability of the beech to stand great wind damage in the gaps was a major factor in its continued survival.

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REGULATORY MECHANISMS IN HOUSE-MOUSE POPULATIONS: THE EFFECT OF LIMITED FOOD SUPPLY ON A CONFINED POPULATION [1]

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The study of factors regulating population growth and maintenance in wild mammals has been handicapped by the complexity of natural environments and the difficulty of controlling or measuring the features of these environments. The house mouse (*Mus musculus*) offers a unique opportunity for circumventing some of these difficulties since its preferred habitat is in man-made structures which can readily be constructed and manipulated in accordance with the demands of experimental procedure. This animal has further advantages as a subject for experimentation in that it breeds rapidly and nearly continuously throughout the year, is relatively sedentary in its habits (Young *et al.* 1950), and tolerates high population densities.

With these advantages in mind a series of studies was initiated with populations of house mice free-ranging within the confines of mouse-proofed rooms equipped with the essential food and shelter requirements.

We would like to thank Howard Young and Arnold J. Petersen for their frequent help in conducting the study, and Joseph J. Hickey and Charles Southwick for their critical reading of the manuscript.

METHODS

The present paper is concerned with a study of the responses of mouse populations to a limited daily food supply. The observations were made during 1949 and 1950 in a vacated unheated army barracks near Madison, Wisconsin. A group of enclosures were prepared by lining the walls of several large empty rooms with sheets of galvanized iron to a height of 22 inches, about six inches higher than the maximum reach of a mouse jumping to escape. A 2-inch turn-in at the bottom prevented gnawing around the edge; there was never any serious attempt at gnawing out elsewhere on the floor.

A total of 8 pens was used; two of these were slightly over 500 square feet in area, and the other 6 approximately 80 square feet in area. The two large pens were each equipped with 4 locations of food and water and 5 units of cover, all symmetrically arranged (Figs. 1, 2).

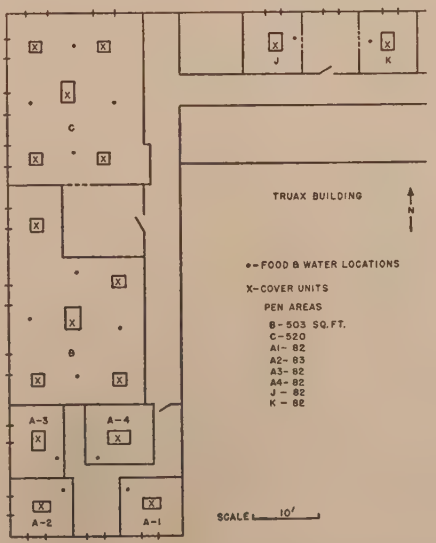

FIG. 1. Floor plan of the building in which the study was conducted, showing the location of food, water, and cover supplies of each pen.

[1] Contribution from the Department of Zoology, University of Wisconsin. The work described in this report was supported by funds from the National Institutes of Health and the Wisconsin Alumni Research Foundation.

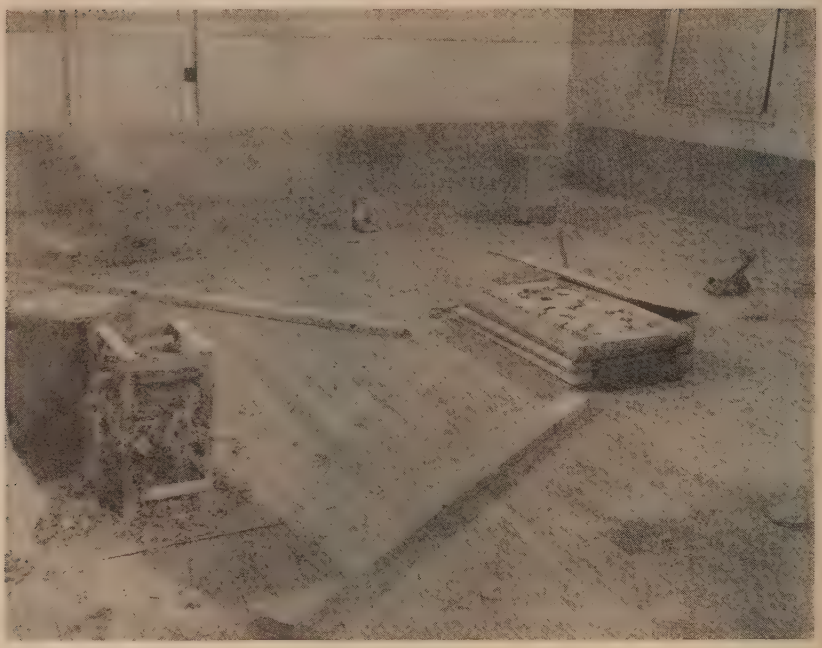

FIG. 2. Photograph of pen B. Two of the cover units are opened to show their construction.

The small pens each had one location of food and water and 1 cover unit.

In the two large pens (B and C) four of the cover units consisted each of an inverted cardboard carton $20 \times 13.5 \times 11$ inches covering a wood frame which supported 5 shelves or floors of Masonite. Nesting material in the form of cotton waste and shredded paper was put on each of the floors. The fifth unit, located in the center of the room, was constructed of three sheets of beaverboard, 36×24 inches, placed one above the other and separated by 2×4 inch boards so as to provide a large, three-storied shelter. Each of the floors was loosely filled with cotton waste and shredded paper. The six small pens each had one cover unit of this latter type, but contained only two layers.

On April 11, 1949, one of the large pens, B, was stocked with 25 male and 25 female mice and the other large pen, C, with 5 male and 5 female mice. All were wild animals live-trapped from natural infestations in Madison.

Both colonies were given 250 grams of food daily, consisting of one part each of rolled oats, ground corn, ground wheat, and powdered commercial rat pellets, 1/4 part of powdered meat scrap, and small amounts of salt and cod liver oil. A fresh lot of food was provided each day and the remainder from the previous day collected for weighing after air drying. Water was provided *ad lib.* in bottles or pans at the four feeding locations; snow was supplied as a supplement in freezing weather.

The six smaller pens were each stocked with 5 male and 5 female mice in mid-October as a supplementary check on the occurrence of reproduction during the winter. These pens were furnished with a surplus of food and water at all times.

All mice were individually marked by toe clipping, no more than two toes being clipped on any one foot. Nestlings too

small to clip with a definite individual pattern were temporarily marked by removing the tip of one toe so that their relationship and place of origin would be known when they were large enough to be marked individually.

A check of the cover units for nestling mice was made every two weeks, and a complete check of all mice in the pens once each month. All mice were weighed and examined for signs of breeding activity and for general condition at each handling. Nestlings were aged according to the criteria given in Table I and marked by litters pending individual marking at a subsequent date. Mice were captured for these check-ups by surrounding each cover unit in turn with a small portable enclosure composed of segments of metal sheeting. Once so enclosed, the cover unit was dismantled, all occupants driven into small box traps, and the partitions checked for nestlings and dead animals. In order to minimize disturbance in the colony and to avoid confusion in the records, the mice from each unit were held in large containers following checking until all units had been examined. The total operation required from one to two hours per pen, and no harmful effects were noted to result from it. This checking procedure proved to be quite thorough; only twice were mice, subsequently shown to have been present, overlooked in the checking operations.

Population Growth

The growth of the populations in the enclosures was traced by direct counts at the monthly censuses, by body weights taken at the same time, and by interpretations of the daily measurements of food consumption.

Figure 3 gives for pen B the monthly census totals, the curve of daily food consumption averaged by weeks, and, from August on, the mass or total weight of the population. The original stock of fifty mice suffered moderate mortality, and no mice were born until the ninth week. At this point (mid-June), with 42 mice present, several litters appeared and the population started a rapid growth which extended for eight weeks until mid-August when it ended abruptly. The form of this growth is seen in the curve of numbers of mice, while the curve of food consumption generally parallels it, although it must be recognized that food consumption does not accurately reflect population numbers when nestlings and immatures with small intake capacities are present. The upward progress of the food-consumption curve was halted abruptly as soon as the total daily supply was being completely utilized during the third week of August. From this point on, food consumption was useful as a population index only after the shortage had been relieved by reductions in the number of mice. The slight residues (8 to 10 grams) recorded during this period consisted of inedible chaff and fecal droppings.

Having reached a peak level shortly after the development of the food crisis, the population started a slow but steady decline. The mass or total weight of the population continued to increase at a slow rate for about three months as the bodily growth of young animals more than compensated for mortality, then leveled off and started a gradual decline parallel to

Table I. *Criteria used in determining the age of nestling house mice.* Data obtained from daily measurements of three wild litters raised in captivity and from published material in Snell (1941).

Age	Criteria
1 to 3 days	Hairless and pink all over.
4 to 6 days	Hairless, but gray dorsally; external ears open.
7 to 9 days	Fine hair dorsally, none ventrally.
10 to 12 days	Fine hair all over; mammae visible in females; eyes still closed.
13 days plus	Ears and eyes completely open; well furred.

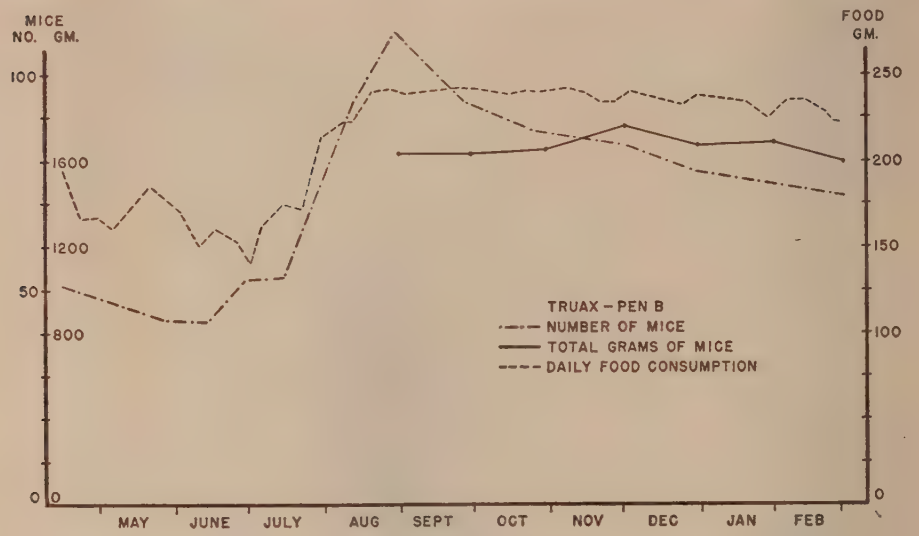

FIG. 3. Changes in the daily food consumption (average for each week), total number of mice (monthly intervals) and total weight of the population (monthly intervals) in pen B.

the slope of the population curve as young mice reached adult size.

Figure 4 presents the monthly census totals, the daily food consumption and the population mass data for pen C where the original stocking comprised only ten animals. As in the larger colony no young were born for nine weeks, by which time three of the animals had died, leaving only four males and three females for breeding. Population growth therefore was slow and, with further mortality during the summer and fall, never reached the capacity of the enclosure as set by the limited daily food supply. The data obtained from this colony are, accordingly, like those from the six small enclosures, primarily useful for supplementary information on reproduction and do not contribute directly to the study of limiting factors.

REPRODUCTION AND SURVIVAL

Detailed records of births and deaths were obtained in the monthly censuses and the bi-weekly checks on reproduction.

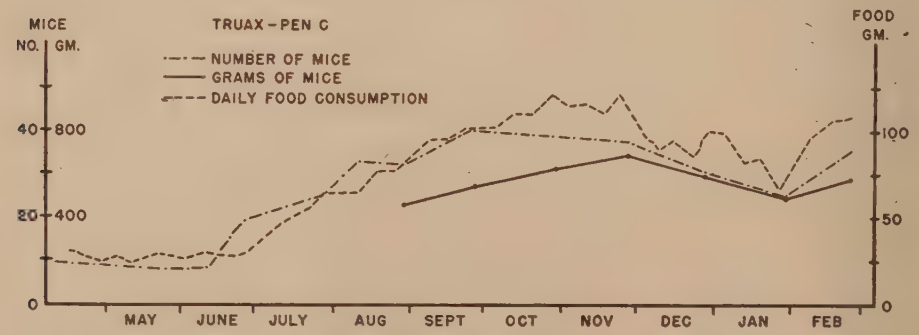

FIG. 4. Changes in the daily food consumption (average for each week), total number of mice (monthly intervals) and total weight of the population (monthly intervals) in pen C.

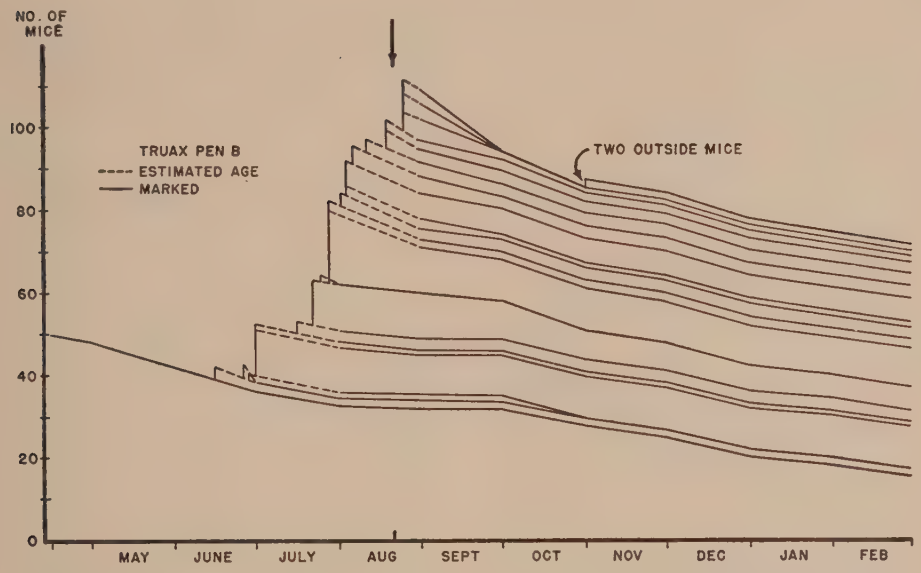

FIG. 5. Numerical composition of the population in pen B and changes in it due to births and mortality. The appearance of each new litter is indicated by a vertical rise from the uppermost line. Solid lines begin at the time of marking of individuals; dashed lines extend the record of litters back to the estimated date of birth.

Figures 5 and 6 present the schedule of litter production and mortality in pens B and C during the eleven months of the study. The appearance of each new litter is indicated by a vertical rise in the top line of the graph, and the size of the litter by the height of this rise. Since daily checking was not feasible, the history of each litter started with its first record which may have been as much as two weeks after birth. The actual date of birth could, however, be estimated with considerable accuracy by the aging criteria presented in Table I and is indicated on the graphs by a dashed extension of the solid line for each litter. Sev-

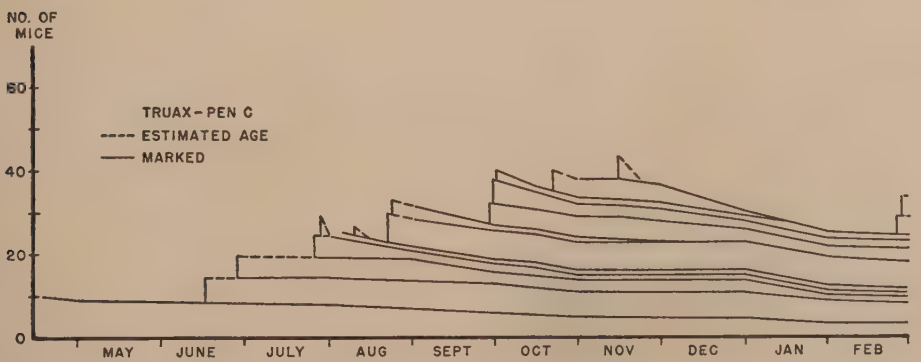

FIG. 6. Numerical composition of the population in pen C and changes in it due to births and mortality. The appearance of each new litter is indicated by a vertical rise from the uppermost line. Solid lines begin at the time of marking of individuals; dashed lines extend the record of litters back to the estimated date of birth.

eral litters were often encountered in a single nest. In most cases these could be easily separated and grouped according to age characters, but in a few instances where this was not possible, the entire group was recorded together. The three large vertical rises during July in Figure 5 (pen B) are due to groupings of litters of this type.

All marked animals which died were recovered in the bi-weekly checks and their deaths dated as accurately as possible within the preceding two-week period. Dead nestlings were similarly dated and recorded whenever found. Additional deaths of nestlings may have occurred and escaped notice as adults are known to eat nestlings on occasion, but no evidence of this was detected in the present study. Total mortality rate is indicated in the graphs by the slope of the uppermost lines to the right. Differential mortality in the various litters and in the adult segment of the population can be traced by following the slope of each line in relation to its base.

As already noted, no young were born in either pen for about 9 weeks. The reason for this delay is not clear, but, in our experience with these and other similar colonies, it seems to reflect a period of adjustment by the mice to the unfamiliar environment and, perhaps, to unfamiliar associates in the colony. These mice, furthermore, were held for up to two weeks before the start of the experiment in large galvanized cans where crowded conditions may have disturbed their normal breeding physiology.

Reproduction, once started, was high in pen B (Fig. 5) during the period of food surplus and then stopped abruptly to produce the deflection in the population curve already noted. Litter size did not change significantly from the inception of this growth period at low levels to its completion at relatively high densities. Litter frequency similarly did not vary in any consistent pattern until reproduction had stopped.

Survival of young mice born before the food crisis had been reached was very high except for the loss of a few animals during the first few days of life (see Fig. 5). Survival among these mice during the period of restricted food supply from Sept. 29 to March 2 was 89%. Adults from the original stock fared less well, losing 17 of their 32 members (53%) during this 5 month period, somewhat more than they had lost during the first five months of the study (33%). Without further data we would hesitate, however, to hypothesize an adverse effect of the food restriction on adult survival. All surviving animals were in excellent physical condition at the termination of the study in March as noted later.

In marked contrast to the good survival of young mice born before the food crisis, 12 of the 13 mice in three litters born shortly after the crisis died within five weeks of birth. The cause of this heavy mortality is not known; it might have been an effect of the food situation on the lactation and maternal care of the mothers. Since many of the animals did not die until after weaning, however, competition for food may have been directly or indirectly involved. No females showed any evidence of pregnancy after these last three litters were born.

Reproduction in pen C (Fig. 6) had a poor start as a result of the early death of two of the five original females, and was further complicated by disease. Several of the litters showed poor weight gains and never contributed to the colony as reproducing individuals. Except for an interruption in December and January, however, litters appeared during every month of the study. Reproduction in the small pens occurred during every month of the winter except December.

Reproductive Activity

The cessation of reproduction in pen B following the food crisis was apparently due to physiological changes in the reproductive tracts of the animals. Data on reproductive activity were obtained by

examination of the external genitalia at the monthly checkings and by dissection of all animals at the conclusion of the study.

In each monthly check females were examined for enlarged mammae and to see if the vaginal orifice was preforate or closed. Female house mice ordinarily become perforate with the first estrous cycle, but the vaginal opening may close again during anoestrous periods and occasionally during pregnancy. Females of adult size (15 grams or more) in pen B showed a drop in the incidence of perforate vaginae from an average of 70% (out of 59 cases) during the three months preceding the food crisis to 17% (out of 58 cases) during the two months that followed. Concurrently in pen C where no food shortage developed the comparable figures were 75% (out of 12 cases) before and 56% (out of 18 cases) after.

No satisfactory criterion of sexual activity in living male mice was found. Testis position, useful with some species, was recorded but proved to have limited value, as the testes moved readily between the scrotal and lower abdominal positions. A decrease in the incidence of scrotal testes in males 15 grams or over from 91% during the period of June through August to 31% during the period from September to January in pen B is suggestive, nevertheless, of a moderate decline in sexual activity. No such decrease occurred in the mice in pen C.

Autopsy data were obtained on all mice surviving to the conclusion of the study on March 2, 1950. Animals from pen B, where population growth had been checked by limited food supply, differed from those in pen C in possessing more fat and in being reproductively quiescent. All mice in pen B had heavy deposits of subcutaneous and abdominal fat while those in pen C had no fat or only slight amounts present. The average daily consumption of food at the time of autopsy was still restricted by the limited supply and still lagged slightly below that of pen C. Deposition of fat under these circumstances of reduced food intake is interesting and may be related to the sexual inactivity which developed at the time of the food crisis. Experimental reduction of food intake in laboratory mice (the same species) has demonstrated a similar increase in fat deposition (Robertson *et al.* 1934) and decrease in reproduction (Evans and Bishop 1922; Ball *et al.* 1947).

Differences in the condition of the reproductive organs in the two pens were also striking. Of the 31 females in pen B all had uteri less than 2 mm in diameter. The ovaries of all were small with no enlarged follicles and no corpora lutea. By complete contrast, nine of the thirteen females in pen C were visibly pregnant, two more had uteri moderately enlarged as in estrus or early pregnancy, and the remaining two were lactating.

Males at autopsy showed a similar though less definite condition of sexual inactivity in pen B. Of the 41 males in that pen, 33 (80%) were active as determined by the size of the seminal vesicles, the presence of visible tubules in the cauda epididymis (see Laurie 1946) and the presence of sperm in stained smears of the testis and epididymis (see Christian 1950). All of the 11 males in pen C, on the other hand, were sexually active by these same criteria. Thus, although males may well have been affected adversely by the conditions in pen B, the female response was far more definite and is believed to be primarily responsible for the cessation of breeding in the colony.

Discussion

The absence of reproductive activity in pen B after mid-August was clearly correlated with the obliteration of daily food surpluses, resulting from population increase. The extent of the actual reduction in food consumption was measured in terms of per capita intake (Table II). These figures show a drop of about 35% in August followed, after September, by a gradual recovery of about a

TABLE II. *Population composition (excluding nestlings) and daily food consumption (average of one week's measurements) at successive monthly intervals in pens B and C*

Date	Number of mice						Daily food consumption			
	Small (under 15 g.)		Large (over 15 g.)		Total		g. per mouse		g. per g. of mouse	
	B	C	B	C	B	C	B	C	B	C
Apr. 29	0	0	48	9	48	9	3.46	3.08	—	—
May 30	0	0	42	9	42	9	4.25	3.41	—	—
June 30	3	0	36	8	39	8	3.97	3.76	—	—
July 29	16	7	35	13	51	20	4.17	3.24	—	—
Aug. 31	38	5	55	17	93	22	2.60	3.52	.15	.19
Sept. 29	40	9	55	18	95	27	2.54	3.72	.15	.20
Oct. 31	14	10	73	23	87	33	2.77	3.68	.15	.20
Dec. 1	4	14	80	23	84	37	2.80	3.24	.13	.18
Jan. 2	1	3	77	28	78	31	3.07	3.19	.14	.17
Feb. 1	0	4	75	21	75	25	3.01	2.54	.13	.14
Mar. 2	0	0	72	24	72	24	3.10	4.44	.14	.20

third of this loss. No such changes occurred in pen C.

These measurements of reduction in consumption per mouse are not entirely representative, however, of the extent of food deprivation in the experimental colony, for the population in August and September contained a substantial number (45%) of young mice under 15 grams in weight with smaller intake requirements. The effect of this change in age and body size composition of the population cannot be measured accurately, but its effect would clearly be to reduce the magnitude of the significance of the drop in per capita intake. Figures on food consumption per gram of mouse are not available for the pre-crisis period, but showed no appreciable change (.15 to .13 grams of food per gram of mouse) during the period from October to March when, as a result of mortality, per capita consumption regained about a third of its previous loss. A comparison with the concurrent intake per gram of mouse in pen C suggests that the deprivation in these terms in pen B may have been somewhat less than 25%. The reduction in intake of adult mice in pen B was probably of this order of magnitude. It occurred at a time, of course, when requirements were probably somewhat increased as a result of lactation (Wang 1925; Richter and Barelare 1938).

The rate at which food deprivation developed in pen B is not obtainable from our data, but it seems probable that the degree of deprivation increased over a period of a week or two after the daily rations were first completely utilized in mid-August as a result of the bodily growth of recently weaned young. By September 1, as indicated in Figure 3, the consumption in terms of grams of food per gram of mouse had stabilized at a fairly constant post-crisis level.

The mechanism by which the development of a food shortage produced a cessation of breeding activity is not immediately clear. Purely physiological factors may have been involved. The studies of Evans and Bishop (1922), Huesby *et al.* (1945) and Ball *et al.* (1947) indicate that moderate fasting will delay or stop the estrous cycle in laboratory rats and mice.

The abruptness with which reproduction stopped suggests that other factors such as social disturbances created by the shortage served as a trigger mechanism in suppressing reproductive functions. In this connection it may be pertinent to note that pronounced changes in behavior and in the diurnal activity rhythm appeared coincident with the development

of the food shortage. Before this, the mice were seldom seen in the daytime, and fed almost exclusively at night. Within a few weeks after it, nearly all of the mice came out to feed as soon as the food dishes had been filled. This was in marked contrast to the concurrent behavior in the neighboring pen C where animals rarely emerged from the shelters until dusk. During the winter months and until the conclusion of the study practically all of the feeding in pen B was done within a period of two hours following the placement of fresh food.

In spite of this concentrated activity and the resultant congestion at the food bowls, there was no conspicuous increase in the amount of fighting and no clear evidence of dominance. This is in agreement with Uhrich's (1938) observations of behavior of white mice under conditions of food deprivation. Some order of precedence may have occurred at the bowls, for small and crippled mice were more in evidence towards the end of the brief feeding periods. But all animals obtained enough food to survive and maintain their body weights.

The success of subordinate animals in securing a fair share of food may perhaps be attributed in part to the intake capacity limitations of dominant individuals at the single feeding period. Had the daily food allotment been distributed in smaller amounts several times during the day, competition might have been more effective, and differential survival rates might have occurred. Any attempt to extend the interpretation of these findings to natural populations should take this possibility into consideration.

Although the cessation of reproduction in pen B was clearly correlated with the development of the food shortage, certain other environmental variables should be considered as possible contributing factors. Among these factors are temperature, crowding, and the amount of cover per individual mouse.

Temperature records were kept from November 11, 1949, to the conclusion of the project in March 1950. During this period temperatures in the building fluctuated between 0° F and 54° F with freezing temperatures occurring on all but 16 nights. Temperatures inside the shelter units averaged considerably higher, especially in the areas surrounding the clusters of resting mice where readings were as much as 60° F above outside temperatures. Mice were, however, obliged to leave such warm microclimates to secure their food and water. This they did hesitantly on cold days as indicated by direct observations and by a significant reduction in food consumption in the other pens where the food supply was not limited (unpublished manuscript).

The effects of low temperature on reproduction and survival in house mice are not clear. Laboratory studies on closely confined rats and mice by Lee (1926), Bohanan (1939), Parkes (1924–25) and Retzlaff (1938) showed a depressing effect of cold temperatures on reproductive activity. Wild house mice, however, are known to breed throughout the year in unheated buildings; Laurie (1946) found them breeding actively in cold-storage rooms at temperatures of − 5° to − 15° F. Parkes and Brambell (1927–28) speculate on the basis of considerable data that cold and a restricted food supply combine to account for the prolonged period of anoestrus in many northern species of wild rodents in winter.

The influence of cold on breeding activity in this study can be isolated, though somewhat imperfectly, from the influence

TABLE III. *Litter production in colonies with an excess of food at all times (colony C and six small pens)*

	No. females over 15 g.	No. of litters born
November	33	3
December	34	0
January	30	4
February	34	12
March 2	34	17*

* Number of females visibly pregnant at autopsy.

of food shortage by an examination of breeding activity in the small pens and in pen C where temperature conditions were the same as in pen B. Reproduction continued with some interruptions in these pens (Table III) during the period of reproductive inactivity in pen B. Thus, cold had a retarding effect on reproduction in all cases; it obviously cannot account in itself, however, for the complete cessation of breeding in pen B.

Crowding was greater and the amount of cover available per mouse was less in pen B than in the others as an inevitable result of the population increase. Other studies now in progress indicate, however, that space *per se* was probably not a factor in the cessation of breeding. Nesting cover was supplied in amounts considered to exceed the requirements of the populations and was apparently more than adequate as indicated by the uneven utilization of the available resources. Of the five cover units in pen B, one or more were generally unoccupied even at the peak of population density. More than half of the animals were often crowded into one unit with pregnant females and nestlings liberally represented.

We conclude that although cold temperatures and crowded conditions cannot be eliminated from consideration, their effects were probably secondary in the definite and sudden response of mice in pen B to the conditions which followed the food crisis. Whether physiological or psychological in origin, this response clearly involved reproductive functions especially in the females, yet did not entail sufficient drain on the energy reserves of the animals to cause loss in weight or viability. Selye (1950, p. 103) has noted that in animals under general stress, reproduction is one of the first functions to be suspended. The gonads, he says (1946, p. 159), undergo atrophy, perhaps the result of a shift in the hormone production of the pituitary to substances, such as the adrenotropic principle, more vitally needed during periods of stress. Both fasting and cold are listed by him as stress factors that can produce this adaptive response. According to this concept it is not surprising that females, with their greater energy demands for reproduction, would respond more completely to stress than males.

Viewing the results of the present study in the light of this concept of adaptation energy, it would seem that the physiological stress of a food shortage acting directly, or indirectly through socio-psychological channels, and bolstered later by the stress of cold, resulted in a shift of energy from reproductive to survival functions. Concurrently in the other pens the stress of cold, acting alone, was not sufficient to suppress reproductive activity.

Although this concept seems to fit the findings here presented it should be extended with caution to natural populations. As stated at the beginning of this paper, an ultimate objective of the study was to analyze the basic factors that underlie population regulation in natural situations. With this in mind an attempt was made to simulate the natural habitat of the species, but in the course of the study certain obvious and important deviations from the natural life situation of the species became apparent. One of these has already been mentioned: by filling the food dishes only once a day an unnatural situation developed along with the food shortage, that of a single concentrated feeding period once each day. The described effects of this on activity rhythms and particularly on competition among colony members is enough, in itself, to invalidate any direct extension of the findings of the study to natural situations. Of greater significance, however, is the confinement factor. While cover facilities may have been more than adequate, and crowding less than that found in some natural habitats, the restrictions to egress, once the stress of food shortage had appeared, must not be overlooked. In a concurrent experiment, with an unconfined population, dispersion occurred as soon as the food

shortage developed, and completely replaced the reproduction response obtained in the present experiment. These observations will be described in another paper.

Summary

Experimental populations of wild house mice (*Mus musculus*) were established in large enclosures with environmental features simulating their natural habitats. Cover and water facilities were supplied in excess, but food allotments were limited to 250 grams per day for each colony. The population in one pen after an initial delay grew rapidly to the limit set by the daily food allotment, then stopped abruptly and gradually declined. The discontinuance of population growth was due to a cessation of reproduction and did not involve any increase in mortality rate of adults or of young born before the food crisis. The cessation of reproduction was due to an interruption of breeding activity particularly in females as indicated by the involution of reproductive organs. No loss in weight or viability occurred, although the per capita consumption of food by adult mice was cut for a time by about one-fourth as a result of the increased number of animals. Feeding rhythms were completely changed by the food shortage and may have contributed to the physiological response through psychological channels.

Populations in the other pens served as controls in considerations of other environmental variables.

It is suggested that the physiological response of the experimental animals may be interpreted in terms of a shifting of adaptation energy under stress from reproductive to survival functions.

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THE FESCUE GRASSLAND IN SASKATCHEWAN [1]

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INTRODUCTION

The dominance of *Festuca scabrella* Torr. in parts of the grassland of western Canada has been noted by various workers. The grasslands of the foothills of southwestern Alberta, the Cypress Hills, and of parts of the aspen grove section were considered by Clarke *et al.* (1942) to belong to a "submontane" type of mixed prairie which they defined as the *"Festuca-Danthonia* Association." Moss (1944) described the grasslands of southwestern Alberta and concurred with the view that the black soils there supported the *"Festuca-Danthonia* Association." In a later paper (Moss and Campbell 1947), however, the presence of *Danthonia* was considered to be associated with the effects of overgrazing, and the grasslands of the black soils of Alberta were described as belonging to the *"Festuca scabrella* Association."

The purposes of the present investigation were to obtain data of a quantitative nature concerning the floristic composition and structure of the vegetation dominated by *Festuca scabrella* in Saskatchewan, to compare these with the composition of fescue communities already described in Alberta, to ascertain the extent of the area dominated by *Festuca scabrella* in Saskatchewan, to relate the fescue vegetation to other major grassland communities of North America, and to characterize the transition of fescue communities with the contacting types of vegetation.

The data presented in this paper were accumulated during 1944 to 1951, but the majority of the intensive field work was done in 1944 and 1950. The two areas concerned are, firstly, the benchlands of the Cypress Hills in southwestern Saskatchewan and, secondly, the part of the aspen grove region (Halliday 1937) lying in a belt averaging about 50 miles in width running in a southeasterly direction from the vicinity of Lloydminster on the Alberta boundary to the vicinity of Saskatoon (Fig. 1).

Grateful acknowledgment is expressed to Mr. J. F. Alex and Mr. A. C. Budd who assisted in the field work, to members of the Saskatchewan Soil Survey who examined the soil profiles, and to the Physics Department of the University of Saskatchewan for weather records. The data from the Cypress Hills were obtained while the senior author was in the employ of the Dominion Department of Agriculture, Experimental Station, Swift Current, while the more detailed studies in the aspen grove region were financed by the Saskatchewan Agricultural Research Foundation.

REVIEW OF LITERATURE

The vegetation of the region concerned in this paper has not been intensively studied. Clements and Clements (1939) observed that grassland in this region is composed of grasses of a circumpolar type, including *Festuca scabrella.* They considered this vegetation as being a counterpart of the submontane type of mixed prairie farther south. Clarke *et al.* (1942) considered the grassland in the black soils of the Cypress Hills and foothills and the grasslands of parts of the aspen grove region to be submontane mixed prairie, dominated by *Festuca scabrella,* with *Koeleria cristata, Agropyron subsecundum, A. trachycaulum, Danthonia parryi,*

[1] This paper is based partly on a thesis presented by the junior author to the College of Graduate Studies of the University of Saskatchewan in partial fulfillment of the requirements for the Master's degree in Plant Ecology.

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D. intermedia, and *Festuca idahoensis* as associates. These authors presented data on composition of the community from three sites in Alberta and one in Saskatchewan which they sampled in conjunction with studies of grazing capacity.

The only other data previously published concerning this grassland community are from Alberta. Moss (1944) described the vegetation in southwestern Alberta where he described the "*Festuca-Danthonia* Association" on black soils in which *Festuca scabrella* (particularly) and *F. idahoensis* were generally dominant, while *Danthonia parryi* and *D. intermedia* were locally dominant. Moss and Campbell (1947) reported on the grassland of the aspen grove region of central Alberta and revised the previous idea that these species of *Danthonia* are climax codominants. They considered the vegetation of these areas to comprise the "*Festuca scabrella* Association" since the dominance of the *Danthonia* species is restricted to areas other than those of intermediate drainage or which have been modified by grazing. Methods involving visual estimation only were employed in these studies.

Bird (1930), in discussing the vegetation of the aspen grove region of western Canada, did not mention *Festuca scabrella.* His field work was conducted in western Manitoba.

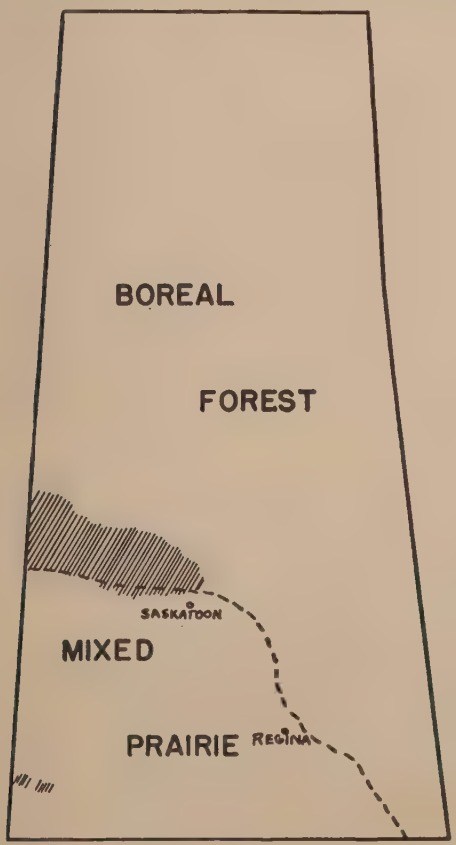

FIG. 1. Outline map of Saskatchewan showing the locations of the regions studied in this paper (hatched areas). The broken line indicates the northern boundary of mixed prairie as mapped by Coupland (1950). The distance from east to west along the boundary with the United States to the south is approximately 390 miles.

DESCRIPTION OF THE AREA

In order to provide a background for the studies of vegetation, a brief description is presented of the region in Saskatchewan in which vegetation dominated by *Festuca scabrella* occurs. Many features of the mixed prairie region, discussed at length in a previous paper (Coupland 1950), are similar to those to be found in the contacting fescue grassland. The chief differences include a slightly cooler, moister climate in the latter region associated with the formation of black soils.

Geology and soils

The aspen grove region was covered by extensive ice sheets and the preglacial sediments, which were once exposed, now underlie a thick mantle of glacial drift. The surface deposits are represented by various types of morainic, glacio-fluvial and lacustrine deposits, glacial till being the most common. They form the parent materials from which the soils of the region have been derived. These deposits are much thinner in the Cypress Hills region than to the northward.

FIG. 2. A rolling part of the aspen grove region about 125 miles northwest of Saskatoon in the black soil zone. *Festuca* is dominant, comprising about 45 per cent of the grassland vegetation, while *Stipa* furnishes about 10 per cent of the cover.

The topography in the region with which this paper deals varies from undulating to rolling (Figs. 2 and 3). Remnants of great terminal moraines occur in the aspen grove region which cause portions of the area to be elevated several hundred feet above the surrounding countryside with the result that the southern margin of the fescue grassland swings farther southward in these areas. Many of the depressions support marshy and saline vegetation, but the broad, saline flats, conspicuous in the mixed prairie region (Coupland 1950), are relatively infrequent in their occurrence.

The soils of areas dominated by *Festuca scabrella* are predominantly black in color of the A horizon. However, within the southern part of the ecotone between the mixed prairie of the brown and dark-brown soil zones and the fescue grassland, this species does dominate to some extent on dark-brown soils as mapped by Mitchell *et al.* (1944, 1950). The soils of the area are discussed fully by the latter authors.

FIG. 3. An undulating area of grassland in the northern part of the dark-brown soil zone 15 miles north of Saskatoon. *Festuca* comprises about 34 per cent of the cover, while *Stipa* makes up another 12 per cent (May 26, 1950).

Climate

The climate is characterized by short, moderately warm summers, by long, cold winters and by a deficiency of moisture. Available weather data for stations in and near the portion of the aspen grove region studied are presented in Table I. Comparable data are not available for the grassland sections of the Cypress Hills, since the measurements there have been made in the forested parts.

Since available soil moisture is very important in determining the type of vegetation which is climax in a region, a considerable difference would be expected in amount of precipitation occurring in areas occupied by mixed prairie and fescue grassland. Such, however, is not the case, since there is only an increase of about 1.5 inches (3.8 cm.) of precipitation between Saskatoon (northern edge of the mixed prairie) and Prince Albert (north of the aspen grove region), which are about 100 miles apart. The difference in moisture effectiveness is considerable, however, as is indicated by the evaporation, that of Prince Albert for the growing season being less than 60 per cent of that of Saskatoon. The months of greatest precipitation are June and July. On the average just less than 70 per cent of the mean annual precipitation falls from May to September inclusive. About 27 per cent of the precipitation falls as snow, much of the moisture from which is lost in runoff.

The prevailing winds are from the west and northwest, and, though east and southeast winds are common, the greater drying influence apparently results from the west winds. This is reflected in the vegetation which is usually more luxuriant on slopes facing northeastward than on those facing the northwest, where they are equally sheltered from the sun.

TABLE I. *Comparison of long-term weather data from stations in and near the aspen grove region of Saskatchewan. The measurements of temperature and precipitation are averaged for periods of 28 to 55 years, while those of evaporation are from 9 to 31 years' records at the various stations*

Environmental factor	North Battleford	Saskatoon	Rosthern	Prince Albert
Temperature (° F.)				
Mean annual	35	34	34	33
Mean, May to September	58	58	57	56
Precipitation (inches)				
Annual	13.41	14.55	14.62	16.11
May to September	9.70	9.80	9.73	10.53
Evaporation (inches)				
May to September	24.8	27.7	24.4	16.3

METHODS AND PROCEDURE

The procedure followed in selection of sites for study and in sampling of the composition of plant communities in these sites was the same as that described in detail by Coupland (1950) in studying the mixed prairie in western Canada.

Several traverses were made of the black soil zone between Saskatoon and North Battleford and of the black soid areas in the Cypress Hills in an attempt to locate sites for study. The principal criterion of selection was the presence of a community differing from any of those of mixed prairie of the brown and dark-brown soils (Coupland 1950). Only those areas were selected for study which had never been cultivated and were relatively unmodified by drifting soil or overgrazing. Sites or parts of sites which were unduly affected by slopes or depressions were avoided, the vegetation on well-drained, level to undulating areas or on moderate slopes being preferred. The areas sampled in each site varied from approximately 10 to 100 acres. Aerial photographs were employed as an aid in the location of areas in which undisturbed sites might be expected to occur, but several of the sites were located by random traverses through the regions. Eleven sites were selected for detailed study in the aspen grove region and four in the Cypress Hills.

Each of the 15 study sites was sampled by means of the point-transect method to obtain data on the percentage of the soil surface occupied by each species of grass and sedge and by the principal forbs and shrubs. Points were projected in groups of 10 at intervals of 25 paces along lines

across each site. A record was made of the point of contact, whether bare soil or base of plant, of each pin at the level of the soil surface. In the case of shrubs, the projection of a point on the soil surface below the crown was considered as a hit. One thousand projections were made in each of the sites in the aspen grove region and 1,500 points were taken in each site in the Cypress Hills.

By calculating the percentage of projections in which the points contacted the base of a species, the basal cover of that species was determined. The percentage of all projected points which contacted the base of all species gave the total basal cover of the vegetation.

Since total basal cover varies considerably between sites in the same community and between different communities, a useful measure for comparison of vegetative types is percentage composition. This was calculated from the point-sampling data by considering the percentage of the total basal cover which is comprised by each of the principal species.

Count-list plots were employed in order to obtain data with respect to the distribution and abundance of forbs and shrubs, which are not well represented in the point-sampling data because of their small basal area relative to crown area and because of their lesser abundance. These were taken equidistantly along transects across the site by dropping a metal frame. The number of plants or rooted shoots of each species was counted in the area enclosed by the frame. This area was one meter square in the case of the sites in the aspen grove region and one meter by one-half meter in the sites studied in the Cypress Hills. Twenty plots were counted in each site. The data were expressed for each species as average abundance (the number of plants or rooted shoots found in 20 plots in a site) and as average frequency (the percentage of the total number of plots in which each species was found). The former is a measure of population density, while the latter indicates the degree of dispersion throughout the community. Use was made of the species area curve (Cain 1938) in deciding that a sufficient number of plots had been counted in each site. By this method the minimum number of square-meter plots required per site in the aspen grove region was found to range from 6 to 12.

In addition to the detailed data obtained by sampling, much information was obtained by visual observations concerning the composition of the vegetation and the distribution of fescue grassland. By this means, changes in vegetative cover were noted in relation to the proximity of depressions, aspen groves and disturbed areas. The extent of the fescue grassland was mapped in a preliminary manner by visual examination of undisturbed sites outside of the region in which the sites were selected for detailed sampling.

An analysis of the root systems of the principal grasses was made by means of the monolith system of Weaver and Darland (1949). In this way, data were collected concerning the distribution of the underground plant parts in various soil layers to a depth of 48 in. (1.2 m.) in four sites.

Hitchcock and Chase (1950) are the authorities recognized for names of grasses. Fernald (1950) is referred to for nomenclature of other families insofar as his manual includes the species of the area. Where these do not occur in Fernald's manual, the nomenclature of Rydberg (1932) is recognized.

The Festuca Grassland

The undisturbed sites chosen for study in the Cypress Hills are dominated by *Festuca scabrella*. In the aspen grove region, the importance of *Festuca scabrella* varies from complete dominance in the northern fringe to a position of codominance with *Stipa spartea* var. *curtiseta* in the northern part of the dark-brown soil zone. The data obtained in the two regions are discussed separtely in order to establish the relationship which exists between them.

The grassland of the Cypress Hills

The *Festuca* community occurs in the Cypress Hills on black soils. The present study of this vegetation must be considered as preliminary and concerns the community which occurs on the "bench" in southwestern Saskatchewan in the vicinity of Cypress Hills Provincial Park. The extent of this community is not large and includes only the relatively level areas above 4,000 feet, where it occupies a narrow belt up to a few miles in width. The sites sampled are all between 4,100 and 4,200 feet in elevation.

In this region, the community is preclimax to the forest of lodgepole pine (*Pinus murrayana*) which occurs on the steep, north-facing slopes of the Hills. It is postclimax to the mixed prairie communities occurring on the more gentle and drier south-facing slopes.

The general appearance of the grassland differs from that of mixed prairie to the north, south and east of the Hills, particularly in the absence of *Stipa* spp. as dominants. The characteristic "sheen" which is provided by the awns of *Stipa* when in head in mixed prairie gives way to a deeper green color of the fescue community since the inflorescence of *Festuca* is not conspicuous (Fig. 4). The fescue vegetation appears to mature much later than does mixed prairie which becomes yellow in late July due to the ripening of the uppermost leaf sheath of *Stipa comata*. The height of the grass exceeds that of the most mesic communities of mixed prairie. The frequency, abundance and vigor of forbs is greater than in mixed prairie, the luxuriance of the vegetation being intermediate between that of mixed prairie (Coupland 1950) and true prairie (Weaver and Fitzpatrick 1934). The abundance of a knee-high shrub, *Potentilla fruticosa,* further characterizes the fescue grassland in the Cypress Hills.

FIG. 4. The above-ground parts of *Koeleria cristata* (left), *Festuca scabrella* (center), and *Stipa spartea* var. *curtiseta.*

TABLE II. *Percentage of basal cover and percentage composition of the total basal cover furnished by each of the principal species and groups of species (exclusive of* Selaginella densa*) in the Cypress Hills section of the* Festuca *grassland. Data are from sampling four sites by the point-transect method*

Species	Percentage basal cover	Percentage composition	
		Including shrubs	Excluding shrubs
Festuca scabrella	6.22	44.1	55.1
Agropyron subsecundum	0.62	4.4	5.5
Danthonia intermedia	0.32	2.3	2.8
Helictotrichon hookeri	0.22	1.6	1.9
Stipa spartea var. *curtiseta*	0.22	1.6	1.9
Other grasses	0.20	1.4	1.8
Carex spp.	2.73	19.3	24.2
Total grasses and sedges	10.53	74.7	93.2
Cerastium arvense	0.17	1.2	1.5
Achillea millefolium	0.12	0.9	1.1
Other forbs	0.48	3.3	4.2
Total forbs	0.77	5.4	6.8
Total vegetation excluding shrubs	11.30	80.1	100.0
Potentilla fruticosa	2.75	19.5	
Rosa sp.	0.05	0.4	
Total vegetation	14.10	100.0	

Three layers of vegetation are present. Below the shrubs, the mid-grass cover is continuous, dominating over the lowest layer of short sedges (*Carex* spp.) and the smaller forbs. *Selaginella densa* forms a discontinuous cover on the soil, where it occupies 5.4 per cent of the surface. It is not uniformly distributed, occurring in only 26 per cent of the 0.5 square-meter plots examined.

The vegetation was sampled by the

point method in four sites and more general observations were made in several others. The average basal cover and percentage composition of each of the principal species and groups of species are presented in Table II. The percentage composition is calculated in two ways, including shrubs in one case and excluding this growth form in the other. The latter calculation is provided to facilitate comparison with the grassland of the aspen grove section where shrubs are much less abundant. The percentage of the soil surface occupied by all species, exclusive of *Selaginella densa,* averages 14.1. The cross-sectional areas of the crowns of shrubs cover 2.8 per cent of the soil surface. The grasses and sedges comprise 93.2 per cent of the non-shrubby cover.

Festuca scabrella occupies an average of 55.1 per cent of the non-shrubby cover in the sites sampled. The next four grasses in abundance, *Agropyron subsecundum, Danthonia intermedia, Helictotrichon hookeri,* and *Stipa spartea* var. *curtiseta,* comprise 12.1 per cent of this cover. The small sedges, comprising 24.2 per cent of the basal cover, are of comparable importance with those in the most mesic community of mixed prairie (Coupland 1950). However, because of their small stature and relatively short season of growth, they are not considered to be dominant despite this large cover. They are here considered as interstitial species.

Secondary species of grasses, each comprising less than 1 per cent of the basal cover, are *Koeleria cristata, Agropyron smithii, Agropyron dasystachyum,* and *Muhlenbergia richardsonis.*

On the basis of basal area as calculated from the point-sampling data *Cerastium arvense* and *Achillea millefolium* are the most abundant forbs. A dwarf species of *Rosa* is the only abundant shrub in addition to *Potentilla fruticosa.*

The abundance and frequency of forbs and shrubs were studied in the same four sites by means of one-half square meter plots. These data are summarized in Table III. They show that 30 species (and groups of species) are sufficiently frequent to occur in 5 per cent or more of the 80 plots. In addition, 20 other species were encountered in sampling.

The dominant, principal, and secondary species which comprise the *Festuca* grassland in the Cypress Hills are arranged below in groups in the approximate order of their abundance (except for the secondary forbs which are arranged alphabetically). The principal grasses and sedges are those making up 1 per cent or more of the total basal cover. The secondary grasses and sedges are those which occur in the sampling data but each of these makes up less than 1 per cent of the basal cover. The principal forbs and shrubs are those which occur in 5 per cent or more of the quadrats counted, while the secondary forbs and shrubs are less abundant but occur in 1 per cent or more of the plots.

TABLE III. *Abundance and distribution of the principal species of forbs and shrubs occurring in the Cypress Hills section of the* Festuca *grassland. Data are from 20 count-list 0.5 meter plots in each of four sites*

Species	No. of plants* per 20 0.5 sq. m.	Percentage frequency
Cerastium arvense	172	92
Achillea millefolium	145	89
Galium boreale	141	75
Viola sp.	30	60
Anemone patens	30	56
Erigeron glabellus	39	39
Oxytropis sp.	30	51
Thermopsis rhombifolia	22	46
Hedysarum alpinum	21	46
Potentilla fruticosa	12	40
Geum triflorum	18	29
Erigeron spp.	27	22
Zizia aptera	11	26
Gaillardia aristata	10	26
Campanula rotundifolia	10	24
Anemone sp.	12	21
Artemisia frigida	12	18
Solidago sp.	8	14
Rosa sp.	10	15
Phlox hoodii	6	9
Astragalus spp.	8	11
Vicia americana	5	9
Vicia sparsifolia	4	10
Solidago glaberrima	5	9
Potentilla camporum	2	18
Potentilla concinna	2	9
Potentilla spp.	3	11
Agoseris sp.	2	9
Dodecatheon sp.	1	5
Selaginella densa	—	26

* The number of plants or rooted shoots.

Dominant grass
Festuca scabrella Torr.
Principal grasses and sedges
Agropyron subsecundum (Link) Hitchc.
Danthonia intermedia Vasey
Helictotrichon hookeri (Scribn.) Henr.
Stipa spartea Trin. var. *curtiseta* Hitchc.
Carex spp.
Secondary grasses and sedges
Koeleria cristata (L.) Pers.
Agropyron smithii Rydb.
Agropyron dasystachyum (Hook.) Scribn.
Muhlenbergia richardsonis (Trin.) Rydb.
Carex spp.
Principal forbs and shrubs
Potentilla fruticosa L.
Cerastium arvense L.
Achillea millefolium L.
Galium boreale L.
Viola sp.
Anemone patens L. var. *wolfgangiana* (Bess.) Koch
Erigeron glabellus Nutt.
Oxytropis sp.
Thermopsis rhombifolia (Nutt.) Richards.
Hedysarum alpinum L. var. *americana* Michx.
Geum triflorum Pursh
Zizia aptera (Gray) Fern.
Erigeron sp.
Gaillardia aristata Pursh
Campanula rotundifolia L.
Anemone sp.
Artemisia frigida Willd.
Solidago sp.
Rosa sp.
Phlox hoodii Richards.
Astragalus spp.
Vicia americana Muhl.
Vicia sparsifolia Nutt.
Solidago glaberrima Martens
Potentilla camporum Rydb.
Potentilla concinna Richards.
Agoseris sp.
Dodecatheon sp.
Selaginella densa Rydb.
Secondary forbs
Allium sp.
Antennaria sp.
Arctostaphylos uva-ursi (L.) Spreng.
Arnica fulgens Pursh
Artemisia camporum Rydb.
Chrysopsis villosa (Pursh) Nutt.
Erigeron pumilus Nutt.
Fragaria sp.
Juncus sp.
Heuchera richardsonii R. Br.
Oligoneuron canescens Rydb.
Potentilla argyrea Rydb.
Potentilla hippiana Lehm.
Potentilla pensylvanica L.
Potentilla sp.
Ranunculus sp.
Sedum stenopetalum Pursh
Sisyrinchium angustifolium Mill.
Zigadenus elegans Pursh

This list includes 9 species of grasses, 2 sedges, 45 forbs, 2 shrubs and one clubmoss.

The grassland of the aspen grove region

The aspen grove region occupies a belt varying in width from 40 to 60 miles in western Saskatchewan. This has often been considered as an ecotone between the grassland formation to the south and the coniferous forest to the north. Critical examination of the vegetation, however, reveals that it consists of an intermingling of grassland and forest communities and that the ecotone occurs only around each grove of aspen (*Populus tremuloides*) within the zone. For this reason, the authors consider the grassland community as distinct from the forest. The proportion of the region which is occupied by grassland increases from north to south. In the northern part of the black soil zone, the forest cover is broken only by occasional small patches of grassland (Fig. 5), while in the south of that zone the aspen groves are scattered throughout the grassland area (Fig. 2) and are finally restricted to depres-

FIG. 5. A small area of grassland in an opening in the aspen forest at the northern edge of the black soil zone approximately 100 miles northwest of Saskatoon. *Festuca* is the dominant, comprising about 54 per cent of the cover (June 16, 1950).

sions. Only the grassland portion of the aspen grove region is discussed in this paper, a study of the forest vegetation of the aspen groves not yet being completed.

The composition of the grassland in the extreme northern part of the region is very similar to that in the Cypress Hills. The outstanding difference is the absence of *Potentilla fruticosa*. The proportion of the vegetative cover contributed by *Festuca scabrella* is approximately the same as in the Cypress Hills. This degree of dominance is maintained farther southward only in the proximity of the groves. Throughout the greater part of the grassland in areas of gently undulating to moderately rolling topography and in soils of medium texture, the relative abundance of *Festuca scabrella* declines and that of *Stipa spartea* var. *curtiseta* increases. Thus in the northern part of the dark-brown soil zone dominance is shared by the two species (Fig. 3). *Festuca* then gives way very rapidly to *Stipa* over the next 10- to 20-mile belt to the edge of the mixed prairie as mapped by Coupland (1950). Throughout all of the black soil zone, however, *Festuca* is much more abundant than *Stipa*.

The *Festuca* community is postclimax to the *Stipa-Agropyron* faciation of mixed prairie (Coupland 1950). The latter commonly occupies exposed locations within the aspen grove region, such as south-facing slopes and tops of knolls. The fescue community is preclimax to aspen forest.

The general appearance of the grassland is the same as in the Cypress Hills except for the absence of *Potentilla fruticosa*. The parts of the region, where *Festuca* forms as large a proportion of the cover as in the Cypress Hills, support a stand of grass as vigorous as in the latter area. With the decline in abundance of *Festuca* southward, an associated decrease occurs in vigor and luxuriance of the vegetation. The absence of the shrub, an associated species, should not be overemphasized in comparing the fescue grassland of the two regions. The composition of the vegetation between the shrubs in the Cypress Hills is so similar to the most vigorous grassland in the aspen grove region that they should un-

doubtedly be considered as the same community. The parts in which *Stipa* is abundant must be considered as transitional to mixed prairie, but over the northern three-quarters of this region *Festuca* is much more abundant that *Stipa*. A gradual increase in the density of the basal cover is associated with the decrease in abundance of *Festuca*. In the most vigorous grassland the basal cover approximates 15 per cent, while this increases to 20 per cent farther southward.

There are two layers of vegetative cover, the mid-grass layer being underlain by species of *Carex* and minor grasses (notably *Bouteloua gracilis* and *Muhlenbergia richardsonis*) as well as by some shorter forbs. *Selaginella densa* occupies a third layer near the soil surface but this is discontinuous, only 3.0 per cent of the soil surface being occupied in the sites sampled. Furthermore, there is a decrease in the abundance of this species from south to north, associated with an increase in the abundance of true mosses.

Shrubs are not abundant in the grassland. However, *Rosa arkansana,* a dwarf shrub seldom more than 4 to 5 inches high but with a deeply penetrating root, occurs only in this habitat. It usually dies down to the ground in winter and renews growth from the base to produce a few leaves and no more than one or two flowers. This is the most abundant shrub in the grassland of this region. *Symphoricarpos occidentalis,* and to a lesser extent *Elaeagnus commutata,* are occasionally scattered throughout the grassland, being adapted for invasion by means of long rhizomes.

The vegetation was sampled by the point method in 11 sites in west-central Saskatchewan. In only one of these does *Festuca* comprise as large a proportion of the herbaceous vegetation as in the Cypress Hills. In 8 others, *Festuca* is much more abundant than *Stipa*. The average basal cover and percentage composition of each of the principal species and groups of species in these nine fescue sites are presented in Table IV. The percentage of the soil surface occupied by all species, exclusive of *Selaginella densa,* averages 16.0. The grasses and sedges make up 91.1 per cent of this cover and the forbs and shrubs the other 8.9 per cent. There is a tendency for grasses and sedges to contribute a larger proportion of the total basal area in the more northerly sites. The cross-sectional area of the crowns of shrubs composes less than 1 per cent of the vegetation.

Three species of grasses and various sedges contribute 77.8 per cent of the total basal area occupied by spermatophytes. *Festuca scabrella, Stipa spartea* var. *curtiseta,* and *Koeleria cristata* are the most abundant species in all these sites, and together on the average compose 53.0 per cent of the basal cover.

In addition to the two species already mentioned, *Agropyron trachycaulum, A. subsecundum, Helictotrichon hookeri, Bouteloua gracilis,* and *Muhlenbergia richardsonis* are the principal species of grasses associated with *Festuca*. Together they contribute 10.2 per cent of the basal

TABLE IV. *Percentage of basal cover and percentage composition of the total basal cover furnished by each of the principal species and groups of species (exclusive of* Selaginella densa*) in the grassland of the aspen grove region of western Saskatchewan. Data are from sampling of nine sites by the point-transect method*

Species	Percentage basal cover	Percentage composition
Festuca scabrella	5.17	32.2
Stipa spartea var. *curtiseta*	1.91	11.9
Koeleria cristata	1.42	8.9
Agropyron subsecundum *Agropyron trachycaulum*	0.52	3.2
Helictotrichon hookeri	0.51	3.2
Bouteloua gracilis	0.42	2.6
Muhlenbergia richardsonis	0.19	1.2
Other grasses	0.50	3.1
Carex spp.	3.98	24.8
Total grasses and sedges	14.62	91.1
Solidago glaberrima	0.23	1.4
Artemisia frigida	0.23	1.4
Anemone patens	0.16	1.0
Antennaria microphylla	0.14	0.9
Phlox hoodii	0.11	0.7
Cerastium arvense	0.10	0.6
Other forbs	0.37	2.4
Shrubs	0.08	0.5
Total forbs and shrubs	1.42	8.9
Total vegetation	16.04	100.0

area on the average, but there is a decrease in the abundance of *Agropyron trachycaulum* and *Bouteloua gracilis*, from south to north. The sedges, notably, *Carex stenophylla* var. *enervis*, *C. pensylvanica* var. *digyna*, and *C. obtusata*, make up 24.8 per cent of the cover. In addition to these, the following secondary species of grasses were recorded in the sampling data: *Agropyron dasystachyum*, *A. smithii*, *Andropogon scoparius*, *Calamagrostis montanensis*, *Danthonia intermedia*, *Festuca ovina*, and *Poa* spp. Each of these species comprises less than 1 per cent of the basal area, and together they furnish 3.1 per cent of the cover.

Analysis of the number of contacts of the metal pins with forbs and shrubs obtained in point sampling shows that *Solidago glaberrima*, *Artemisia frigida*, *Anemone patens*, *Antennaria microphylla*, *Phlox hoodii*, and *Cerastium arvense* make up 68 per cent of the non-grassy cover. The most abundant shrub, *Rosa arkansana*, comprises 3 per cent of this area. The remaining 29 per cent of the non-grassy cover is furnished by 14 species of forbs and 3 species of shrubs in the data on basal area, contributing 26 and 3 per cent, respectively.

The abundance of forbs and shrubs was studied in the same 9 sites by the use of count-list quadrats. These data are summarized in Table V. They show that 33 species (or groups of species) of forbs and 2 shrubs are sufficiently frequent to occur in an average of 5 per cent or more of the 180 meter quadrats. In addition 32 other species were encountered in sampling.

The dominant, principal, and secondary species which comprise the grassland in the sites studied in the aspen grove region of western Saskatchewan are arranged below in groups in the approximate order of their abundance (except for the secondary forbs and shrubs where the arrangement is alphabetical).

Dominant grass
- *Festuca scabrella* Torr.

Principal grasses and sedges
- *Stipa spartea Trin.* var. *curtiseta* Hitchc.
- *Koeleria cristata* (L.) Pers.
- *Agropyron trachycaulum* (Link) Malte
- *Agropyron subsecundum* (Link) Hitchc.
- *Helictotrichon hookeri* (Scribn.) Henr.
- *Bouteloua gracilis* (H.B.K.) Lag.
- *Muhlenbergia richardsonis* (Trin.) Rydb.
- *Carex stenophylla* Wahlenb. var. *enervis* (C. A. Mey.) Kukenth.
- *Carex pensylvanica* Lam. var. *digyna* Boeckl.

Secondary grasses and sedges
- *Agropyron dasystachyum* (Hook.) Scribn.
- *Calamagrostis montanensis* Scribn.

TABLE V. *Abundance and distribution of the principal species of forbs and shrubs occurring in the aspen grove section of the* Festuca *grassland. Data are from 20 count-list quadrats in each of nine sites in the Saskatoon-North Battleford region*

Species	No. of plants* per 20 sq. m.	Percentage frequency
Solidago glaberrima	619	64
Cerastium arvense	397	51
Achillea millefolium	225	54
Anemone patens	151	77
Aster ericoides	163	42
Antennaria microphylla	134	46
Galium boreale	135	32
Artemisia frigida	64	54
Artemisia ludoviciana var. *gnaphalodes* / var. *pabularis*	68	38
Geum triflorum	70	39
Rosa arkansana	50	38
Androsace sp.	32	44
Astragalus spp.	25	37
Potentilla pensylvanica	27	22
Campanula rotundifolia	23	24
Antennaria campestris	29	18
Thermopsis rhombifolia	22	17
Comandra pallida	22	16
Vicia sparsifolia	14	18
Heuchera richardsonii	9	25
Erigeron spp.	20	20
Solidago rigida	11	9
Phlox hoodii	10	7
Potentilla concinna	4	13
Oxytropis macounii	5	11
Orthocarpus luteus	6	9
Arabis hirsuta	5	9
Ranunculus sceleratus	5	9
Potentilla gracilis var. *pulcherrima*	5	8
Cogswellia villosa	5	7
Symphoricarpos occidentalis	4	6
Viola adunca	3	7
Equisetum laevigatum	2	5
Selaginella densa	—	50

* The number of plants or rooted shoots.

Danthonia intermedia Vasey
Agropyron smithii Rydb.
Festuca ovina L.
Andropogon scoparius Michx.
Poa spp.
Carex obtusata Lilj.

Principal forbs and shrubs
Solidago glaberrima Martens
Cerastium arvense L.
Achillea millefolium L.
Anemone patens L. var. *wolfgangiana* (Bess.) Koch
Aster ericoides L.
Antennaria microphylla Rydb.
Galium boreale L.
Artemisia frigida Willd.
Geum triflorum Pursh
Rosa arkansana Porter
Artemisia ludoviciana Nutt. var. *gnaphalodes* (Nutt.) T. and G.
Androsace sp.
Astragalus spp.
Potentilla pensylvanica L.
Campanula rotundifolia L.
Antennaria campestris Rydb.
Thermopsis rhombifolia (Nutt.) Richards.
Comandra pallida A. DC.
Vicia sparsifolia Nutt.
Erigeron sp.
Heuchera richardsonii R. Br.
Solidago rigida L.
Phlox hoodii Richards.
Artemisia ludoviciana Nutt. var. *pabularis* (Nels.) Fern.
Potentilla concinna Richards.
Oxytropis macounii (Greene) Rydb.
Orthocarpus luteus Nutt.
Arabis hirsuta (L.) Scop. var. *pycnocarpa* (M. Hopkins) Rollins
Ranunculus sceleratus L.
Potentilla gracilis Dougl. var. *pulcherrima* (Lehm.) Fern.
Cogswellia villosa (Raf.) Schult.
Symphoricarpos occidentalis Hook.
Erigeron glabellus Nutt.
Viola adunca Sm.
Equisetum laevigatum A. Br.
Selaginella densa Rydb.

Secondary forbs and shrubs
Agoseris scorzoneraefolia (Schrad.) Greene
Anemone multifida Poir.
Arabis sp.
Aster laevis L.
Aster sp.
Chenopodium album L.
Chrysopsis villosa (Pursh) Nutt.
Cirsium sp.
Elaeagnus commutata Bernh.
Erigeron caespitosus Nutt.
Erysimum inconspicuum (S. Wats.) MacM.
Fragaria sp.
Gaillardia aristata Pursh
Gentiana amarella L.
Gentiana strictiflora (Rydb.) Greene
Gutierrezia diversifolia Greene
Hedysarum alpinum L. var. *americanum* Michx.
Juncus balticus Willd.
Lychnis drummondii (Hook.) S. Wats.
Penstemon gracilis Nutt.
Penstemon procerus Dougl.
Petalostemon purpureum (Vent.) Rydb.
Plantago rugelii Dcne.
Polygonum convolvulus L.
Potentilla arguta Pursh
Potentilla flabelliformis Lehm.
Senecio sp.
Solanum triflorum Nutt.
Spiraea alba Du Roi
Zigadenus elegans Pursh
Zizia aptera (Gray) Fern.

The above list includes 15 species of grasses, 3 sedges, 62 forbs, 4 shrubs and one clubmoss.

In two of the sites selected for study on dark-brown soils, *Stipa* was found to be as abundant as *Festuca*. The data obtained from point sampling indicated that the principal associated grasses are the same as in the sites dominated principally by *Festuca*, except for the rarity of *Muhlenbergia richardsonis*. The count-list data show that the principal non-grasses are the same, the first 11 listed in Table V,

being the 11 most abundant species in these sites.

Discussion

The data presented in this paper establish the fact that the *Festuca scabrella* association (Moss and Campbell 1947) of the black soils of southwestern and central Alberta does extend eastward into the black soils of Saskatchewan, in the Cypress Hills in the south and the aspen grove section in the north. The dominance of *Festuca scabrella* throughout this range is the major characteristic of the vegetation. Certain associated species are not widely distributed. *Danthonia parryi,* which Moss and Campbell have considered as a major disclimax species under grazing in Alberta, is rare in Saskatchewan. Instead, the disclimax species increasing with overgrazing are various components of the preclimax contact, the mixed prairie. In the fescue grassland of Saskatchewan overgrazing causes an increase notably in *Stipa* spp., *Bouteloua gracilis,* and *Artemisia frigida.* The greater influence of the mixed prairie on the fescue community in this region is thereby indicated.

An attempt was made to ascertain the extent of distribution of the fescue grassland in the aspen grove section of Saskatchewan beyond the boundaries of the region represented by the study areas sampled. These efforts were not successful in establishing with any degree of certainty that this type of vegetation is climax any farther eastward than Saskatoon. The presence of postclimax communities associated with elevated areas of land and with sandy soils east of that city complicated the task of locating suitable study sites. Sufficient observations have been made in the black soils of southeastern Saskatchewan from the United States boundary to the latitude of Yorkton (150 miles northward) to suggest that the ecotone between the fescue grassland to the northwest and the true prairie (Weaver and Fitzpatrick 1934) to the southeast is very wide and varied in composition. Its character is modified by the invasion of components of mixed prairie from the southwest. Thus in this region, small areas dominated by *Stipa spartea* var. *curtiseta, Stipa comata, Agropyron* spp. and *Bouteloua gracilis,* alternate with communities in which *Festuca scabrella* and associates of the fescue community are abundant and with others in which species of the true prairie, notably *Andropogon scoparius,* are conspicuous. The complexity of these vegetative types requires further consideration.

Several of the observations of Moss and Campbell (1947) in Alberta are corroborated by the present study. The latter authors note the decreasing abundance of *Potentilla fruticosa* in the fescue grassland from the United States boundary northward along the foothills. This species is rare in the fescue belt in the aspen grove region of Saskatchewan but is abundant in the Cypress Hills in the south.

Moss and Campbell stated that *Festuca* and *Stipa* communities occur intermixed in the dark-brown soil zone of Alberta. The present study indicates that in west-central Saskatchewan, the occurrence of the *Festuca-Stipa* complex is limited to a 10- to 15-mile wide zone in the northern part of the dark-brown soil zone but occupies much of the grassland area of the black soil zone.

The work of Moss and Campbell indicates that the *Festuca* grassland is more fully developed to the west of the area concerned in the aspen grove region in the present paper. They described *Festuca scabrella* as growing "almost to the exclusion of other higher plants." Many of the data presented here do not support this view, since the dominant only occupies an average of 32 per cent of the basal cover in the aspen grove region of Saskatchewan. However, in the site in the latter region where this species is most abundant, it comprises 54 per cent of the vegetation, and similarly in the Cypress Hills the proportion of the non-shrubby layers furnished by this species is 55 per cent. Since Moss' data were based on visual estimates accurate comparison is

not possible between the two regions. However, it is the experience of the present authors that a site, in which 40 to 50 per cent of the basal cover is composed of *Festuca scabrella,* appears to be almost exclusively occupied by this species. For this reason, the assumption is here made that the *Festuca* communities of the Cypress Hills and the most vigorous fescue communities of the aspen grove region of Saskatchewan are very similar in the degree of dominance of *Festuca scabrella* to the grassland which was studied in Alberta. This agrees with the observations which the senior author has made in brief visits to parts of the region studied by Moss and Campbell. The parts of the aspen grove region where *Festuca* reaches a degree of dominance and vigor similar to that in the Cypress Hills are limited to the northern fringe of the grassland. For this reason, the conclusion may be reached that the major part of the area dominated by this species in the Saskatoon-Lloydminster region (west central Saskatchewan) supports a community comparable with much of the transition zone which Moss and Campbell found on dark-brown soils in Alberta. This opinion is supported by the abundance of *Stipa spartea* var. *curtiseta* in the Saskatchewan sites while the Alberta reports indicate that this species is only occasional in the *Festuca* community farther westward.

Taking these factors into consideration, the distribution of the *Festuca* grassland north of the Cypress Hills in Saskatchewan must be restricted to only the northern part of the aspen grove region. Consequently, much of the black soid zone in Saskatchewan is occupied by a transitional type in which *Festuca* is associated with some abundant subdominants from mixed prairie. The transition zone, which is found in the dark-brown soil zone in Alberta, thereby is located largely in black soils farther eastward. This situation explains the absence of the *Festuca* community to the east of Saskatoon, except as small patches, and supports the observations that have been made of the increasingly deep penetration which the species of mixed prairie have made into the black soil zone farther eastward. The smaller size of tussocks found in much of the Saskatchewan grove region as compared with those in Alberta also supports the view that the fully developed *Festuca* grassland wanes in western Saskatchewan.

Another indication that the fescue grassland of western Saskatchewan's aspen grove belt is not as fully developed as that of Alberta is the rarity of *Danthonia parryi* in the former region. Moss and Campbell consider this species as forming an edaphic climax within the zone dominated by *Festuca scabrella* in Alberta. The numbers of species of various growth forms presented by Moss and Campbell are greater than those listed in the present paper. This does not necessarily indicate a reduced luxuriance since the means of obtaining the former data were by visual examination, while the species listed in this paper are limited to those encountered in sampling. The observations of the senior author, however, support the statement of Moss and Campbell concerning the reduced number of associated species in this grassland northward and eastward from southwestern Alberta.

The admission must be made that the lack of full expression of dominance of *Festuca* in some of the sites studied may be the result of grazing. Although care was taken to choose areas for study which showed as little evidence as possible of modification, the accuracy of the criteria used may be questioned. Moss and Campbell have admirably discussed the effects of grazing and mowing on this community in Alberta.

The dominance of *Festuca scabrella* in the grasslands of the black soils of Alberta and western Saskatchewan results in the presence of a grassland community which does not fit into any of the six associations of the grassland formation of North America as defined by Weaver and Clements (1938). The latter authors do not mention *Festuca scabrella* as an important component of any association. For

this reason and since information concerning the composition of these grasslands was not available when they proposed their classification, the suggestion is hereby made that the *Festuca* grassland of western Canada be considered as a seventh grassland association, in the Clementsian sense, namely, the *Festuca scabrella* Association. Recognition must be given to Moss and Campbell (1947) for the proposal of this name, but they failed to suggest that the community be considered as a major entity in the sense that Clements used the term "association." Their reference to the "*Stipa comata* Association" in the same paper for one consociation of mixed prairie supports the implication that their meaning was more confined with respect to the status of the fescue grassland.

Characteristics of Festuca scabrella

The autecology of the principal grasses of the fescue grassland has been discussed in a previous paper (Coupland 1950) dealing with these species in the brown soil zone of Saskatchewan and Alberta. Detailed information on the behavior of these species in the moister (fescue) region of the grassland is not available. Observations indicate that development is principally affected by the shorter growing season in causing later commencement of growth in the spring. The moister conditions associated with slightly higher precipitation and lower evaporation probably compensate for this by postponing the dormant stage of dry summer until a later average date. The environmental conditions, however, favor *Festuca scabrella* over all other species.

Festuca scabrella Torr. is a bunch grass producing tufts of long, filiform, permanently involute leaves and a rather narrow panicle on a relatively long culm. Both leaves and culms tend to be erect at the base. In most of the sites studied in the Saskatoon–North Battleford region, the crowns do not exceed 5 to 6 inches (13 to 15 cm.) in diameter, the larger of these consisting of a ring of small tufts surrounding a mass of dead leaf and stem bases. The description by Moss and Campbell (1947) of the crowns of this species ranging up to 10 to 20 inches (25 to 50 cm.) in diameter in Alberta is a further indication that the fescue grassland does not thrive in the Saskatchewan aspen grove belt as well as to the westward.

The foliage reaches a height of 7 to 8 inches (18 to 20 cm.) in exposed areas and 14 to 15 inches (36 to 38 cm.) in sheltered places, such as near the groves. Similarly, culms reach heights of 14 in. to 3 ft. (3.6 to 9.1 dm.) in different parts of the community. The most vigorous fescue is located in the Cypress Hills and near the northernmost part of the black soil zone in the aspen grove region. In these areas its vigor compares with that in the black soils of western and central Alberta.

The roots are densely distributed, rather dark in color, and penetrate more deeply than do those of *Stipa* and *Koeleria*. The development of the individual root behind the zone of development of root hairs is characterized by the suberization of the endodermis to produce an impervious layer. The cortex then de-

Table VI. *Characteristics of the three major grass species of the fescue grassland in relation to seed production. Data are from one site in 1950 about 11 miles north of Saskatoon*

Characteristic	*Festuca scabrella*	*Stipa spartea* var. *curtiseta*	*Koeleria cristata*
No. of plants counted	9	10	10
Ave. no. of inflorescences per plant	6	—	5
Ave. no. of spikelets per plant	127	20	227
Ave. no. of flowers per spikelet	4–6	1	2–4
Ave. no. of flowers per plant	500–760	20	450–900

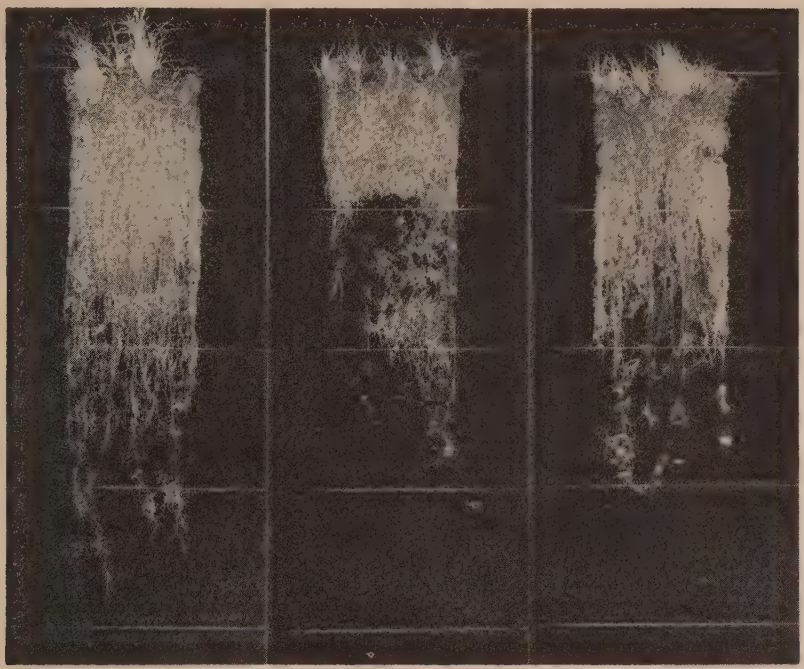

FIG. 6. Root systems of *Festuca scabrella* (left), *Stipa spartea* var. *curtiseta* (center), and *Koeleria cristata*. These are from 3-inch thick monoliths of black soil, 12 in. across and 4 ft. deep. The horizontal white lines indicate intervals of 1 foot in depth.

cays to leave the cutinized epidermis, still with root hairs, free from the stele.

The leaves exhibit xerophytic modifications. They are permanently involute in such a way that they appear to be terete in cross section. The exposed dorsal surface bears a heavy, cuticularized epidermis, some cells of which are papillose and produce the characteristic rough feeling. This epidermis bears no stomata and is underlain by a thick sclerenchymatous layer. The ventral surface is deeply furrowed and is protected from air movement by folding of the leaf. A few hairs provide further resistance to movement of air. At the bottom of each groove are two or three rows of bulliform cells, forming a hygroscopic pulvinus. A row of stomata occurs along either side of this zone. The ridges between the grooves are supported by "I-beams" of sclerenchyma connecting with the dorsal sclerenchymatous layer. The main vascular bundles lie in these beams, and smaller ones run through the zone of mesophyll which surrounds each groove.

Data were obtained with respect to seed production of *Festuca, Stipa,* and *Koeleria* in one site in the transition zone 11 miles north of Saskatoon. These are presented in Table VI.

DEVELOPMENT OF THE UNDERGROUND PARTS OF GRASSES

The development of the root system of *Festuca* was investigated in four sites, while that of *Koeleria* and *Stipa* was studied in two of these. The weights of the underground parts per volume of soil are greatest in the case of *Festuca,* where the greatest depth of penetration also occurs. The depth of *Festuca* in the soil profiles studied exceeded 4 ft. (1.2 m.) in each instance, while the roots of the other two species were restricted to a depth of 3 to 4 ft. (Fig. 6). The roots ex-

TABLE VII. *Distribution of the underground parts of three species of grasses in each soil layer below 0.25 sq. ft. of soil surface by oven-dry weight in grams. Percentage of the total weight found in each layer to 48 inches is also given*

Depth (in.)	*Festuca*		*Stipa*		*Koeleria*	
	Weight (gm.)	Percentage	Weight (gm.)	Percentage	Weight (gm.)	Percentage
0–6	42.48	73.4	25.33	71.4	25.35	66.7
6–12	6.94	12.0	6.51	18.4	6.27	16.5
12–18	4.03	7.0	1.54	4.3	3.21	8.4
18–24	1.98	3.4	1.35	3.8	1.44	3.8
24–30	1.36	2.4	0.26	0.8	1.34	3.5
30–36	0.55	1.0	0.43	1.2	0.37	1.0
36–42	0.37	0.6	0.05	0.1	0.04	0.1
42–48	0.13	0.2	—	—	—	—
Total	57.84	100.0	35.47	100.0	38.02	100.0
No. of samples	4		2		2	

tended slightly less deeply on the moister sites (black soils) than in the more xeric areas (dark-brown soils). The average weight of oven-dried underground parts was ascertained to a depth of 4 ft. in nearly pure stands of each species. For *Festuca,* the average was 57.84 gm. per cu. ft. of soil, while the corresponding data for *Stipa* and *Koeleria* were 35.47 and 38.02 gm., respectively. On the average, 15 per cent more root material occurred to a depth of 4 ft. in black soils as compared to dark-brown soils.

A summary of the data accumulated with respect to distribution of roots in various arbitrary soil levels is presented in Table VII. These indicate that the total weight of the root material under stands of *Festuca* is approximately 50 per cent greater than under *Stipa* and *Koeleria.* They also indicate the large proportion of the root system which is concentrated near the soil surface. An interesting comparison with similar data from stands of *Andropogon* spp. in eastern Nebraska as presented by Weaver and Darland (1949) is made in Table VIII. Both species of *Andropogon* are dominants in various communities of true prairie.

TABLE VIII. *A comparison of the distribution of underground parts of* Festuca scabrella *by weight in various soil layers in Saskatchewan with that of two grasses of the black soils of eastern Nebraska* (Weaver and Darland 1949)

Soil layer (inches)	Saskatchewan		Nebraska*			
	Festuca scabrella		*Andropogon gerardi*		*Andropogon scoparius*	
	Weight (gm.)	Percentage	Weight (gm.)	Percentage	Weight (gm.)	Percentage
0–6	42.48	73.4	31.34	74.6	44.83	80.8
6–12	6.94	12.0	4.79	11.2	4.35	7.6
12–24	6.01	10.4	3.77	8.9	3.92	7.0
24–36	1.91	3.4	1.62	3.6	1.85	3.3
36–48	0.50	0.8	0.68	1.4	0.69	1.2
48–60	—	—	0.17	0.3	0.06	0.1
Total	57.84	100.0	42.37	100.0	55.70	100.0
No. of samples	4		7		2	

* From Weaver and Darland (1949) who worked with samples approximately two per cent smaller than those used in the present study.

TABLE IX. *Oven-dry weight of underground parts of three species of grasses in each major soil horizon in the* Festuca *grassland in Saskatchewan. The percentage of the material in each horizon to a depth of 48 inches is calculated*

Soil horizon	Ave. thickness (in.)	*Festuca*		*Stipa*		*Koeleria*	
		Weight (gm.)	Percentage	Weight (gm.)	Percentage	Weight (gm.)	Percentage
A and A–B	6.8	42.60	73.6	23.44	66.1	23.32	61.4
B	20.2	13.41	23.2	11.52	32.5	13.74	36.1
C or D	21.0	1.83	3.2	0.51	1.4	0.96	2.5
Total		57.84	100.0	35.47	100.0	38.02	100.0
No. of samples		4		2		2	

The distribution of the root system by weight according to soil horizons is presented in Table IX. A comparison with the data of Weaver and Darland (1949) shows that they obtained an average of 85.3 and 87.8 per cent of the root material, respectively, from *Andropogon gerardi,* and *A. scoparius* in the A horizon, the average thickness of which was 12.2 and 11.5 inches, respectively. The smaller percentage of root material obtained in the A horizon in the present study is associated with the thinner horizon, which averaged only 6.8 inches. These data indicate that the distribution of grass roots may be more closely associated with depth than with soil horizon.

Although generalizations are hazardous from as few samples as were taken in this study, some tendencies are shown from further analysis of the data. The amount of root material contributed by *Festuca* to a depth of 48 inches in black soils is about one-third more than in the dark-brown soils sampled. Deeper penetration of roots of these three species tends to be made in the dark-brown (drier) soils.

The distribution of the root system under stands of *Festuca* in the Cypress Hills was studied by the method outlined in a previous paper (Coupland 1950). One-half square meter blocks of soil removed to a depth of 4 inches in three sites contained an average of 6.60 tons of underground plant parts per acre. In two sites, the amount in the 4- to 8-inch layer averaged 0.71 tons per acre.

These data indicate the large quantities of root materials which occur in grassland. The yield of underground parts of *Festuca* averages 11.11 tons per acre to a depth of 48 inches in the aspen grove region. This material influences greatly the development of soils.

SUCCESSIONAL COMMUNITIES

Many changes in vegetation associated with disturbance and variations in topography were observed during the course of this study. Postclimax communities of aspen, willow, or grasses occur in depressions and on protected slopes (Fig. 7) and preclimax communities of mixed prairie species are located in exposed habitats.

In many depressions, the changes in vegetation are much more conspicuous than are those of relief. Depressions of considerable extent are often occupied by

FIG. 7. Fescue grassland occupying relatively level land, a south-facing slope and crest of a knoll. Note the influence of protection afforded on the north-facing slope as reflected in the vegetation.

sedge (*Carex* spp.) meadows surrounded by belts of aspen (*Populus tremuloides*) and willow (*Salix* spp.). Smaller ones support only groves of aspen, while in the smallest ones where difference in relief is less pronounced, only changes in the grass cover occur. The complex relationship between the aspen community and the grassland has not been studied. The purpose here is to outline changes in the composition of the grass cover in and near shallow depressions within the fescue community.

With increasing moisture supply, the first noticeable change in vegetation is an increase in the relative abundance of *Festuca scabrella* and the disappearance of *Stipa*. *Artemisia frigida* disappears, while an increase occurs in the abundance of *Solidago glaberrima* and *Galium boreale*. At this point, within the transition region with mixed prairie, the fescue community is approximated as described by Moss and Campbell (1947) and as found in the Cypress Hills and northern part of the aspen grove region. With further increase in moisture supply, *Muhlenbergia richardsonis* often forms nearly pure stands and *Artemisia ludoviciana* var. *gnaphalodes* and *Antennaria* spp. become more abundant. At moister levels, stands of *Danthonia intermedia* are common, and *Artemisia ludoviciana* var. *pabularis* is frequent. Still moister situations support *Agrostis* spp. The level of this stage may be only two or three feet below the climax community. Further depression results in the appearance of shrubs. Other species which increase in abundance in shallow depressions include *Agropyron trachycaulum, Stipa viridula, Solidago rigida*, and *Anemone canadensis*.

The sheltering effects of the groves of aspen are considerable. The reduction in wind velocity and accumulation of snow associated with these areas are reflected in the composition of the grassland adjacent to them, particularly on the (east) side leeward with respect to the prevailing winds. Species which are noticeably more abundant in such areas include *Danthonia intermedia, Muhlenbergia richardsonis, Spiraea alba, Solidago rigida*, and *Zigadenus elegans*.

Detailed information has not been obtained concerning plant succession in this area after fire, heavy grazing, land abandonment, and other disturbances. This has been discussed in adjacent grassland areas (Moss and Campbell 1947; Coupland 1950).

Summary

Quantitative data are presented concerning the composition and structure of the fescue grassland in Saskatchewan. On the basis of an analysis of these, the grassland of the Cypress Hills and the northern fringe of the aspen grove region in Saskatchewan is apparently part of the *Festuca scabrella* association as described by Moss and Campbell (1947) in southwestern and central Alberta. In these areas, which are limited to the more moist black soils, *Festuca scabrella* occupies 55 per cent of the basal cover provided by herbs. The principal subdominants are *Agropyron subsecundum, Agropyron trachycaulum, Danthonia intermedia, Helictotrichon hookeri, Koeleria cristata, Muhlenbergia richardsonis, Stipa spartea* var. *curtiseta*, and *Carex* spp. The principal forbs are *Cerastium arvense, Achillea millefolium, Galium boreale*, and *Anemone patens*. In the Cypress Hills, the presence of an abundant shrub, *Potentilla fruticosa*, is characteristic.

The spermatophytes in the *Festuca scabrella* association occupy 14.1 per cent of the soil surface. The grasses comprise 69.0 per cent of the non-shrubby layers. Sedges are abundant, occupying 24.2 per cent of the herbaceous cover, but are not dominant because of their dwarf habit and short season of growth.

The grassland associated with most of the aspen grove region in Saskatchewan is a transitional type between the *Festuca scabrella* association and the *Stipa-Agropyron* faciation of the mixed prairie (*Stipa-Bouteloua* association) as described in a previous paper (Coupland

1950). This zone is about 40 miles wide. In this area *Stipa spartea* var. *curtiseta* is codominant with *Festuca scabrella* in the northern dark-brown soils. With penetration of the black soil zone a rapid transition to the *Festuca scabrella* association takes place until *Festuca* finally becomes the only dominant. Within the transition zone many associated species are those typical of mixed prairie. Notable among these are *Solidago glaberrima* and *Artemisia frigida.*

The modifications in the vegetative cover associated with depressions and the proximity of groves of *Populus tremuloides* are characterized. Within the transition zone, a slight increase in moisture causes a shift to the typical *Festuca scabrella* community.

The distribution of the root systems of *Festuca scabrella, Stipa spartea* var. *curtiseta* and *Koeleria cristata* is described in relation to depth and soil horizon.

The conclusion is reached that the *Festuca scabrella* community of Alberta and western Saskatchewan cannot be considered to be allied to any of the six grassland associations previously described in North America (Weaver and Clements 1938) and should therefore be considered as a seventh association of the grassland formation.

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NOTES AND COMMENT

TEMPORAL VARIATION IN A SMALL COMMUNITY OF AMPHIBIANS AND REPTILES

During the past five years we have been able to make a rather intensive study on a population of amphibians and reptiles inhabiting a small stretch of woodland lying just south of Gainesville, Alachua County, Florida. Our house is situated just at the edge of this wooded area, or "hammock," and the region of study has been, in effect, our back and side yards. Our observations on the fauna here have yielded data not only on the life histories and habits of the animals but also on the structure of a community with particular reference to its amphibian and reptile constituents.

The study area is a plot roughly rectangular in shape and approximately a third of an acre in extent on the border of a typical North Florida mesic hammock. The most conspicuous and abundant trees are water oaks (*Quercus niger*). In addition there are black gums (*Nyssa sylvatica biflora*), sweetgums (*Liquidambar styraciflua*), hickories (*Hicoria*), blue beeches (*Carpinus caroliniana*), and one large loblolly pine (*Pinus taeda*). At the edge of the hammock are several live oaks (*Quercus virginiana*). The undergrowth in the area, which consisted mainly of seedling oaks, palmettos (*Sabal minor*) and vines, was largely cleared out, but the leaf mold has been left undisturbed. In addition, a small pool, which is merely a cement-lined depression approximately four feet by three feet by four inches deep, was constructed near the eastern edge of the lot.

The area is bounded on the west by an old field in which some seedling loblolly pines have become established. To the north lies a dense thicket which slopes gently down to a swampy area drained by a drainage ditch which in turn empties into a permanent stream about 150 yards from the study area. To the east lies the main body of the hammock which includes a temporary pond and a good-sized permanent pond. The study area is thus capable of being invaded by the amphibians and reptiles of several diverse ecological situations.

Observations on the amphibians and reptiles of the area were more or less random from the time we moved in, November, 1946, until the following June when we began to keep a Journal, listing at that time all species of those two classes that we had so far observed. For the next year and a half we recorded only those species that were new or rare in the area, but in January, 1949, we began recording for each day all species of amphibians and reptiles seen during the day. The yard is inspected regularly morning and night and at random times during the day so that for two and a half years it has been under almost constant daily observation.

The following list gives the amphibians and reptiles recorded in the area from November, 1946 to June, 1951. Those species marked with an asterisk were all that were seen during the first two years.

**Amphiuma means means* (two-toed amphiuma)
**Triturus viridescens louisianensis* (Louisiana newt)
**Ambystoma talpoideum* (mole salamander)
**Manculus quadridigitatus* (dwarf salamander)
**Scaphiopus holbrooki holbrooki* (spadefoot toad)
**Bufo terrestris terrestris* (southern toad)
**Acris gryllus dorsalis* (Florida cricket frog)
**Hyla cinerea cinerea* (green tree frog)
**Hyla crucifer bartramiana* (southern spring peeper)
Hyla femoralis (pine woods tree frog)
**Hyla ocularis* (little chorus frog)
**Hyla squirella* (squirrel tree frog)
**Eleutherodactylus ricordi planirostris* (greenhouse frog)
**Rana catesbeiana* (bullfrog)
Rana clamitans (bronze frog)
Rana grylio (pig frog)
**Rana pipiens sphenocephala* (southern leopard frog)
**Microhyla carolinensis carolinensis* (narrow-mouth toad)
**Anolis carolinensis* (Carolina anole)
**Sceloporus undulatus undulatus* (southern fence lizard)
Cnemidophorus sexlineatus (six-lined race runner)
**Lygosoma laterale* (ground lizard)
**Eumeces laticeps* (broad-headed skink)
**Rhadinea flavilata* (yellow-lipped snake)
**Heterodon simus* (southern hog-nosed snake)
Opheodrys aestivus (rough green snake)
**Coluber constrictor priapus* (southern black racer)
Elaphe guttata (corn snake)
**Elaphe obsoleta quadrivittata* (chicken snake)
Cemophora coccinea (scarlet snake)
**Natrix sipedon pictiventris* (banded water snake)
**Storeria occipitomaculata obscura* (southern red-bellied snake)

Thamnophis sirtalis sirtalis (garter snake) (*vide* Conant 1951)
**Micrurus fulvius fulvius* (coral snake)
**Chelydra serpentina osceola* (snapping turtle)
Terrapene carolina bauri (box turtle)
Pseudemys nelsoni (Nelson's terrapin)
**Pseudemys scripta scripta* (pond terrapin)

We have here a rather large list of a relatively small group of animals recorded on a small area over a period of time. We have therefore taken the opportunity to analyze it in terms of the ratio of genera to species present in relation to time. Such an analysis at the outset has certain weaknesses because of the taxonomy of the forms involved. There is still a question, for example, as to whether the little chorus frog, here listed as *Hyla ocularis,* should be placed in the genus *Hyla* or *Pseudacris.* Nonetheless, we feel that our data point to rather definite conclusions on the ecological problems of the number of species in relation to genera.

There has recently been a great deal of interest in this general ecological problem and the different viewpoints have been adequately presented by Elton (1946) and Williams (1947, 1951). Bagenal (1951) is critical of both of the above workers, however, on the grounds that the data on which their conclusions are based are not suitable to the type of analyses to which they have been subjected. One of his criticisms is that several of the communities discussed by them have been investigated over long periods of time during which the composition of the fauna might change. Since our data seem to demonstrate quantitatively that the genus : species ratio in a small community does change in relation to time, we wish to present them for consideration.

Table I gives the total number of genera and species of amphibians and reptiles and the relationship of genera to species for one day, for two years, and for four years and seven months. The data for one day are not of a single day but are instead the average of thirty-six days. These thirty-six days are the 1st, 10th and 20th of each month from June 1, 1950 through May 31, 1951. In this manner typical days of all seasons of the year are brought into consideration. The average number of species and genera recorded on the thirty-six days were 6.06 and 5.72 respectively.

Examination of this table shows that, as we study a small area over increasing periods of time, we add species proportionately faster than we do genera so that the average number of species per genus increases as time goes on. Even though the changes with time indicated in this table do not show statistical significance by the Chi-square test, we believe that the trend may be of biological significance. Obviously, larger samples are much to be desired, and we hope that this report will stimulate others to collect similar data.

From our observations we believe that the change in ratio with time results primarily from one fact, namely that the environmental factors continually vary so that the area is at different times suitable for different kinds of animals. These changes vary from short term, such as wet and dry weather, to more regular ones of longer duration such as winter and summer. Finally, we are able to recognize differences from year to year.

Examination of the species list will reveal that there are forms recorded here that any competent herpetologist would consider incompatible in so far as habitat is concerned, for example, *Amphiuma* and *Sceloporus.* This is, of course, perfectly true, but it serves to emphasize the point that this area (and probably most small areas) is not occupied by a single community but rather by a succession of communities. At the time the *Amphiuma* was recorded the yard was temporarily flooded from severe hurricane conditions and animals such as *Amphiuma, Chelydra,* and *Natrix* were able to invade the area for a short period of time. On the other hand, during more normal times forms like *Sceloporus* may be present in abundance.

This alteration of environmental conditions, hence communities, further convinces us that there is no valid excuse for eliminating any form recorded in an ecological survey on the basis that it is only an "occasional transient." So far as we are able to determine, the common garter snake, *Thamnophis s. sirtalis,* does not reside in our area. The fact remains, however, that soon after a good colony of *Rana* becomes established at the pool at least two

TABLE I. *Variation in species-genus ratio in relation to time in a small area*

Time	Genera with 1 species	Genera with 2 species	Genera with 3 species	Genera with 4 species	Genera with 5 species	% Genera with one species	Avg. No. sp./g.
1 day (avg.)						94	1.06
2 yrs.	22	1	0	1	0	92	1.16
4 yrs. & 7 mo.	25	2	0	1	1	86	1.31

different garter snakes (they have been seen at the same time) move in to make a feast thereon. This has been observed on several occasions. Since these snakes utilize the protoplasm of the community as a food supply it seems to us that they should definitely be considered part of it even though they may be on the area for only fifteen or twenty minutes at a time and have their modal places of abode elsewhere. The same thing is true for the black racer, *Coluber c. priapus,* which we occasionally see foraging in the yard, and probably for most of our transient visitors.

On only ten of the days of the thirty-six used in obtaining the average for one day were there more species than genera present. In each of these ten instances the increase was brought about by the fact that both *Hyla cinerea* and *Hyla squirella* were recorded. When both are present at once, however, there is a rather sharp ecological separation with *cinerea* occurring on palmettos and other low shrubs while *squirella* occurs rather high in the trees. Numerous times we have had tree frogs invade the house by way of the chimney, which terminates among the tree tops, but every time except one it has been a *squirella* rather than a *cinerea.* The other Hylas, when they are to be found at all, occur in or on the leaf mold except *femoralis* which is the only one that has been seen on the big pine tree. *Hyla crucifer* is normally present in number only in periods of flood, while *femoralis* was taken only during a severe drought.

The only two genera present of which we have ever recorded two species in the same day are *Hyla* and *Rana.* As pointed out above, there is good ecological separation between the Hylas. Since the Ranas occur at the only artifact present, the pool, we have not been able to get as good separation there. The usual *Rana* present is *clamitans,* but on some occasions we have had two species at the same time. For a while three young *catesbeiana* lived at the pool with an adult *clamitans,* and several times we have had a young *sphenocephala* living for a few days there when it was occupied by one or more *clamitans.*

In conclusion, we have over the years come to feel (1) that our back yard forms, at least in so far as amphibians and reptiles are concerned, a more or less compact ecological unit which is occupied by communities formed basically of one species per genus; (2) that these communities are not stable but vary with environmental conditions. As conditions change, certain species abandon the community and others become part of it. The longer the period of time involved, the more diverse the environmental conditions that can obtain, hence the increasing number of species that can and do utilize the area as a habitat and therefore, for the time being, become part of the community. As time goes on and new species are added to the fauna of this small area there is an increasing probability that they will be species of genera previously recorded rather than species of genera heretofore unrepresented.

One other point to be mentioned is that we feel it incumbent upon anyone making an ecological or faunal survey of a small area to state precisely the period and amount of time involved since the components of the community change from time to time as conditions change, although the geographic area remains the same.

Summary

A study was made of the amphibian and reptile constituents of the community of a small area in northern Florida over a period of four years and seven months. It was found that species of amphibians and reptiles abandoned or moved into the area as environmental conditions changed. While at any one period the average number of species per genus was quite low, with cumulative time the average for the area increased. This is attributed to the fact that the area is not occupied by a single community but rather by a succession of communities as environmental conditions change.

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THE USE OF 2,4-D IN THE CONTROL OF WATER HYACINTH AND ALLIGATOR WEED IN THE MISSISSIPPI DELTA, WITH CERTAIN ECOLOGICAL IMPLICATIONS[1]

Introduction

Water hyacinth (*Eichhornia crassipes* Solms.) and alligator weed (*Alternanthera philoxeroides* (Mart.) Griseb.) constitute a weed problem of the first rank in the lower Gulf of Mexico coastal area of the United States.

Water hyacinth is usually free-floating and grows in fresh water. It may completely cover water surfaces, impeding boat navigation and causing reduction of the oxygen content of the water so that game fish cannot live. It is known to reproduce from seeds but vegetative propagation by means of root stalks is more common. Because of their free-floating habit, water hyacinths are readily dispersed in water.

Alligator weed grows in the moist soils of the delta and floodplains of the Mississippi and other rivers, as well as in shallow fresh and brackish water, as a rooted emergent. It makes its most luxuriant growth in shallow water where there is a mud bottom. In deeper water, approximately three feet and over, alligator weed is generally confined to a zone a few feet wide along the bank in which it is rooted. However, if there is a mat of water hyacinths established, it may root in this mat and so advance over deep water. Alligator weed is not known to reproduce from seeds, but it increases readily by vegetative means. Stems may be as much as 6 feet long and nodes are 6 to 8 inches apart. Shoots and adventitious roots may arise from each node. Like the water hyacinth, the alligator weed is transported readily by water. Free-floating pieces grow but little, but they remain alive and resume growth when they reach a substratum in which to root.

As a terrestrial plant in the new alluvial soils of the Mississippi delta, alligator weed sometimes grows in nearly pure stands, but usually it is associated with other plants. Some combinations in which it was found in connection with this study, named according to the chief species, are: alligator-cattail (Typha); alligator-roseau (*Phragmites communis* Trin.); alligator-bullrush (*Scirpus californicus* (C. A. Meyer) Britton, *Scirpus validus* Vahl.); alligator-cutgrass (*Zizaniopsis milacea* (Michx.) Doell and Aschers); alligator-sedge (*Cyperus erythrorhizos* Muhl., *C. virens* Michx., *Rynchospora corniculata* (Lam.) A. Gray); alligator-willow (*Salix nigra* Marsh). The lands of the lower delta are subject to flooding almost every year when the river is high, and that time a layer of silt is deposited. Alligator weed withstands burial in the silty deposit very well and hence it has become well-established in it.

Hitchcock *et al.* (1949) have reported on a series of tests to determine the value of 2,4-D and other chemicals in the control of water hyacinth and alligator weed. Most of the tests reported were made under controlled conditions in small pits, but some were made under field conditions. The present paper is a report on the results of applications of the amine salt of 2,4-D, largely by means of helicopter, in weed-infested areas of the following types: borrow pits, drainage ditches, a shallow lake, a small distributary of the Mississippi river, and two areas of new land in the outer delta of the Mississippi. The use of the helicopter for this purpose has been discussed by Zimmerman *et al.* (1950). The studies were made during a period from July, 1949, to June 15, 1950. The following were observed in the field: species of plants present and an estimate of their relative abundance in each of the areas before it was treated with chemical; the capacity of 2,4-D to destroy water hyacinth and alligator weed under the conditions applied; the effect of the chemical on other species of plants; changes in environmental conditions due directly or indirectly to the treatments; and successional changes occurring when either of the two weedy plants was reduced in an area.

Some of the areas considered are between New Orleans and Ponchatoula, Louisiana, in older delta which is not now subject to annual flooding from the Mississippi river. Other areas are in the Delta National Wildlife Refuge, in a section where annual flooding, with consequent deposition of silt, occurs. All of the areas are at or very near sea-level in elevation; the water-table is near the surface. Soils are clays or silts.

For convenience the areas are considered in several categories, according to the conditions and problems.

Aquatic Habitats

Borrow pits and deep drainage ditches

Borrow pits and deep drainage ditches have the common condition of containing water to a depth of from about 3 to 15 feet throughout the year. Water hyacinths can float freely in them. The borrow pits studied parallel highways and were formed when soil was removed to build up the road beds. They are usually 30 to 50 feet wide and many are navigable to small boats. About 20 miles of borrow pits and a half mile of deep drainage

[1] The work here reported was carried out under a contract between Tulane University and the U. S. Corps of Engineers.

ditch were sprayed. These distances are linear measurements and do not consider total area. One flight with the helicopter over a ditch or pit was generally sufficient to cover it from bank to bank.

In some instances, the infestation in the waterway was nearly pure water hyacinth; again it was nearly pure alligator weed; or it may have been a mixture of the two. The problem is different in each case.

A borrow pit which was infested with almost pure water hyacinth parallels the Airline Highway (U. S. 51) between Moisant Airport and Norco, Louisiana. It was sprayed in mid-October, 1949, in 5 sections, each about 0.8 mile long, with 2,4–D of concentrations of 5, 10, 15, 20, and 40 per cent free acid equivalent. These concentrations resulted in applications of about 1, 2, 3, 4, and 8 pounds, respectively, per acre. The results are summarized in Table I, Area 1. Herbicide applied at a rate of one pound per acre killed about 90 per cent of the water hyacinths but they did not disintegrate and sink. Rather, they remained in place throughout the period of observation, about 6 months. The following spring regrowth began, and by June the surface of the pit was again covered with living plants. Not only did one pound of 2,4–D per acre fail permanently to reduce the number of water hyacinths, because of such rapid regrowth, but it contributed to the formation of a flotant of dead hyacinths in which other plants, particularly willows, ferns, and pennyworts, may germinate and grow. The only way to remove such a flotant is by mechanical means because the mat is bound together by roots and will not sink.

There was no significant difference between the results of the treatments with 2 and with 3 pounds per acre. In both cases, it required 150 days for the plants to sink and by that time there was considerable regrowth. Plants treated at a rate of 4 pounds per acre sank in 90 days and hence regrowth was less than at the lower concentration. The reason for this is explained below. Sinking occurred within 28 days in that area sprayed at a rate of 8 pounds per acre. This treatment can be considered as adequate. But even at this concentration, a few plants escaped and some respraying would be necessary to have a complete kill of the plants.

Regrowth of hyacinths occurs in two ways. There are almost always a few plants which are missed when spray is applied, as suggested just above. Secondly, parts of plants such as submerged rootstalks often are not completely killed, and unless carried to the bottom by the rest of the plant when it sinks will produce new plants. Sinking of the plant before regrowth begins is essential if maximum benefit is to be derived. It follows that treatment in late summer, or fall, or winter, when regrowth is slow, would be superior to treatment in early summer when regrowth is rapid.

In October, 1949, a section of about 15 miles of a borrow pit between LePlace and Ponchatoula, Louisiana, was treated with 2,4–D at a rate between 1½ and 2 pounds per acre. The weed infestation was a mixture of alligator weed and hyacinth. The results of the treatment are summarized in Table I, Area 2.

Only the most exposed parts of the alligator weeds were killed. Most of the water hyacinths were killed, but as was the case with the low concentration sprays along the Airline Highway, they required 150 days to sink. During that time the alligator weeds prospered; they had little competition from living hyacinths, and they had the support of the dead flotant mass. The weed growth had changed from mixed water hyacinth and alligator weed to nearly pure alligator weed.

During March and April, 1950, some of the pit just discussed above was again sprayed, part with one and part with two applications of 2,4-D. Each application was at a rate of 8 pounds per acre. It was applied from a boat. When the spray was applied the alligator weed was so thick in places that it was necessary to open a path for the spray boat by means of a cutter boat, a device used extensively in the past to mechanically destroy hyacinths and alligator weeds. By June the amount of weed was reduced to a fringe 3 to 4 feet wide along each bank. The remaining plants were yellow-green in color and were not growing rapidly (see Table I, Area 3).

In waterways, 2,4-D, when effective, destroys alligator weed in two ways. Parts of plants extending above the water are killed, and attachments along the bank are broken if they are above water level. It is evident that both of these processes would occur best at time of low water when more of the plant is out of water.

During none of the earlier observations of the borrow pit along the ponchatoula highway was any water lettuce (*Pistia stratiotes* L.) seen. In June, 1950, water lettuce was present in quantities to cover about 1 per cent of the water surface in some places. In Louisiana, water lettuce seems to be incapable of competing successfully with water hyacinth and alligator weed and removal of these species enabled water lettuce temporarily to increase.

Area 4 and 5, Table I, is a large drainage ditch about two miles from Kenner, Louisiana. It was treated with 2,4-D in October, 1949, at a rate of something under 4 pounds per acre. Only the most exposed stems of alligator weed were killed, and regrowth was rapid. In mid-January, 1950, it was sprayed again, at a rate of 10 pounds per acre. More plants were killed

TABLE I. *Treatment of water hyacinths and alligator weeds in aquatic habitats with 2,4-D*

Type of area	Specific area	Type of infestation	Treatment		Percentage plants killed (estimate)	Time until sinking	Regrowth	Evaluation of treatment
			Date	Pounds per acre				
Borrow pit	1. Airline highway	Water hyacinth	Oct./49	1	90	No sinking	Complete by June, 1950	No value; actually harmful
				2	90	150 days	50% in 150 days	No value
				3	92	150 days	50% in 150 days	No value
				4	95	90 days	Slow, but significant amount	Inadequate treatment unless more used in few months
				8	99 plus	28 days	Slight in 8 months	Adequate treatment; followup needed
	2. LaPlace-Ponchatoula	Water hyacinth-alligator weed	Oct./49	1½–2	Hyacinth—90, Alligator—25	150 days	To more than original in 150 days	Inadequate
	3. Same as area 2	Alligator weed	Mar., Apr./50	8	95	60 days	Slow	Both treatments adequate but need to be repeated when regrowth occurs; water lettuce appeared in area
				16	95	60 days	Slow	
Deep drainage ditch	4. Two miles north of Kenner	Alligator weed	Oct./49	4	40	No sinking	To original condition by Jan., 1950	No value
	5. Same as area 4	Alligator weed	Jan./50	10	90	No record	Considerable by June, 1950	Adequate, but must be repeated for permanent value
Shallow ditch	6. Clancy ranch	Alligator weed	Oct./49	2	20	No sinking	Complete in 90 days	No value
				8	50	No sinking	Complete in 90 days	No value
Shallow lake	7. Labranch	Water hyacinth	July/49	1–4	99	Nearly all in 120 days	Regrew where they did not sink	Good, but higher concentration of chemical would have been better; considerable increase of *Potomogeton* and *Najas*
			Oct./49	1–4	99	90% in 150 days	Regrew where they did not sink	
Distributary Miss. River	8. Long Island bayou	Alligator weed	July/49	8	99	40 days	Back to 25% original in 11 months	Adequate, but needs to be repeated about once a year until alligator weed is eradicated

and regrowth was not rapid but by June there was again a growth extending out 3 to 6 feet from each bank.

It is evident from these reports that alligator weed is difficult to eradicate with 2,4-D, when it is growing in waterways. Treatments at a rate of 2 to 4 pounds per acre were ineffective. Eight pounds or over reduced the amount of alligator weed materially but did not eradicate it completely. It appears that several treatments at 8 pounds or over per acre would be required to kill all of the weed.

Shallow ditches

A ditch on the ranch of Sheriff Clancy, located near Kenner, Jefferson Parish, was so badly infested with alligator weed that stems had matted down and formed an almost solid layer about 6 inches deep. Two miles of the ditch was sprayed in mid-October, 1949, half at a rate of 2 pounds per acre and half at a rate of 8 pounds. Stems contacted with the more concentrated spray were killed and they turned brown. Stems contacted with the less concentrated spray were killed but turned only yellow-green. Neither treatment gave any lasting value. Regrowth was very rapid (Table I, Area 6).

Shallow lake

A shallow lake near Labranch station on the I.C. Railroad has an area of about 400 acres. It varies in depth from approximately 1½ to 6 feet. Part of it occupies an abandoned drainage project and formerly was a field. Part was a cypress swamp and many cypress trees (*Taxodium distichum* (L.) Richard) grow in it still. It is reported that until about 1940 the lake was an excellent place for fishing and duck hunting. Then a protective levee broke, permitting factory wastes to enter. This contamination, it is believed, was the cause of the dying out of the fish and the plants which furnished food for ducks. During the time that the levee was broken, water hyacinths entered and soon they became numerous. By 1949, they covered approximately a third of the surface of the lake. They formed an almost solid cover over the part which had been a cypress swamp, and a belt about 200 to 300 feet wide encircled most of the rest of the lake. Large rafts of hyacinths drifted back and forth with changing winds.

On July 19, 1949, 95 gallons of 20 per cent 2,4-D was applied to a part of the lake. This resulted in an actual application of from 1 to 4 pounds per acre, varying with the altitude at which the helicopter had to fly to avoid the trees, and with the horizontal distance from the helicopter. Actually, no particular effort was made to avoid spraying the trees. In mid-October, 1949, 200 gallons of 2,4-D was applied, the concentration and rate of application being as in the first. With the second spray, most of the infested part of the lake had been covered. But many areas were missed entirely and others received little chemical. The results are summarized in Table I, Area 7.

Most of the plants treated in July died but, due to the generally low concentration of chemical, sinking was slow. Most of them had sunk by November, after about 120 days. A few plants of those treated in October began to sink in November, but most were slower. Sinking continued all winter and by March about 90 per cent of all plants had sunk. It is important to note here that water hyacinths sank in water only 1½ feet deep. Regrowth began in March, and the final 10 per cent never sank.

An important change accompanying water hyacinth reduction in this lake was the increase in the submerged vegetation. In the summer and fall of 1949 there was no indication of the presence of pondweed (*Potomogeton*) nor leafy pondweed (*Najas*). By the winter, small amounts of both were seen. In June, 1950, *Potomogeton foliosus* Raf. and *Najas flexilis* (Willd.) Rostk. & Schmidt, both excellent duck foods, were present in amounts said not to have been equalled since water hyacinths came into the lake.

As was stated earlier no special effort was made to avoid spraying the cypress trees. Leaves were killed but no permanent damage resulted (see Table III). New leaves soon apeared. Some cypresses which lost leaves following the October spray were growing new ones in November when most unsprayed trees had lost theirs for the winter.

Distributary of the Mississippi River

Long Island Bayou is a branch of Main Pass, one of the main distributaries of the Mississippi, and empties into the Gulf of Mexico. Near its origin, the bayou is about 40 feet wide, but it becomes smaller as it breaks up into more distributaries. At time of high water, it has considerable current; at time of low water it rises and falls with the tide and is somewhat brackish. Throughout most of its length, it was infested with alligator weed which fringed both banks with a strip 4 or 5 feet wide. Where the bayou became narrower the fringes met in the middle.

An application of 8 pounds per acre in July, 1949, resulted in almost complete clearing of the bayou in 40 days (Table I, Area 8). There was some regrowth but the bayou remained rather free from alligator weed through the winter. By June, 1950, the amount was back to about 25 per cent of what it had been 11 months

TABLE II. *Treatment of alligator weeds in moist silts of the lower Mississippi River delta with 2,4-D*

Specific area	Treatment		Percentage plants killed (estimate)	Regrowth	Evaluation of treatment
	Date	Pounds per acre			
1. Lieter's Bayou	July/49	1	50	Complete by June, 1950	No value
		2	60	Complete by June, 1950	No value
		4	80	Considerable by June, 1950	Little value
		8	99	Well-started by June, 1950	Repeated treatments necessary if value is to last
2. Dave's Pond	July/49	1	50	Same as Lieter's Bayou for corresponding concentrations	Same as Lieter's Bayou for corresponding concentrations
		2	60		
		4	80		
		8	99		

before. It is believed that an adequate treatment of this bayou once a year would keep it free of alligator weed.

Moist Silt Habitats

Two areas in the Delta Game Refuge, of the U. S. Fish and Wildlife Service, were selected to be treated with 2,4-D. One was along Lieter's Bayou and the other was near Dave's Pond. Four parallel strips were treated in each area, one at a rate of 1 pound per acre, one at 2 pounds, one at 4 pounds, and one at 8 pounds. The results are summarized in Table II.

At 8 pounds per acre there was almost complete killing of all parts of alligator weeds that extended above the ground. With the 4 pound treatment, exposed stems were killed but prostrate stems close to the ground escaped, as they apparently were protected somewhat by other plants. The 2 and the 1 pound treatments did not kill all of the exposed plants and those close to the ground escaped.

Regrowth occurred in all of the areas treated, the rate being, roughly, inversely proportional to the concentration of chemical used. The differences between the 4 strips decreased with time and by June, 1950, it was not possible to distinguish one area from another, nor the treated from the untreated areas.

It is evident that a single application of 2,4-D, even at 8 pounds per acre, is not effective against alligator weed growing in the moist silts of the delta. Because of the dense mat of plants not all stems are contacted with spray, and there is evidence that 2,4-D is not translocated downward in alligator weed stems more than a few inches.

Evidence pointing to the short distance through which lethal amounts of 2,4-D are translocated in alligator weed was seen in observations made in December, 1949. Eighteen plants, all of which had received the treatment at 8 pounds per acre, and all of which had been killed back to the ground level, were dug up. All were sprouting. The number of sprouts varied from 1 to 12 per plant, with an average number of 4.4. The uppermost sprouts emerged from the stems at distances as little as a half inch and not over 5 inches from the soil surface. Completely lethal dosages of 2,4-D had not been translocated more than 5 inches in these plants and in most cases it was much less. The maximum distance of translocation was not more than 2 internodes. This is in agreement with the findings of Earle *et al.* (1951) who measured the distance and rate of translocation of 2,4-D-C^{14} in alligator weed. They found the radioactive material moved to

TABLE III. *Effects of 2,4-D on certain species associated with water hyacinths and alligator weeds*

Species	Pounds 2,4-D per acre	Effect
Cyperus erythrorhizos	8	All plants killed
Cyperus virens	8	All plants killed
Phragmites communis	8	No effect
Rynchospora corniculata	8	All killed
Salix nigra	8	Small trees 3 to 6 feet tall quite dead in 5 weeks; branches on larger willows killed back to region of about 1 inch diam.
Scirpus californicus	4	About half killed
	8	All killed
Scirpus validus	4	About half killed
	8	All killed
Taxodium distichum	1–4	Leaves on trees of all sizes killed but no permanent damage done to woody branches
Typha	8	Healthy plants appeared unharmed but some with insect infestation appeared further weakened

the top of each plant, but downward only 1 to 2 internodes. We had no way of determining how far upward the 2,4-D had moved.

A single application of 2,4-D had no lasting effect on alligator weed in the lower delta, as just described. Actually it may have done more harm than good by destroying some competitors. These are indicated in Table III. Small willows and sedges were generally killed. Unfortunately, *Phragmites communis*, which grows in many parts of the delta and seems to be worthless as food for animals, was not harmed at all by 2,4-D.

Summary

Water hyacinths can be killed and sunk under any conditions in which they grow in south Louisiana by applications of 8 pounds per acre (free acid equivalent) of the amine salt of 2,4-D. Treatment in late summer or fall when the rate of growth is slow is preferable to treatment in spring and early summer. A follow-up treatment to eliminate any plants which escaped the first is important. Elimination of water hyacinths from a shallow lake resulted in a greatly increased quantity of submerged vegetation, principally *Potomogeton* and *Najas*.

A single application of 2,4-D at 8 pounds per acre did not give complete elimination of alligator weed from borrow pits and deep ditches but it did reduce the amount considerably. A second application further reduced it and brought it under control. It is not known how many applications would be needed to eliminate all alligator weed from such water ways.

In shallow ditches in the older delta and in new soils of the younger delta, where alligator weed attains its rankest development, 2,4-D had no significant value in destroying the weed.

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EFFECTS OF WEATHER CONDITIONS ON HORSEFLY POPULATIONS [1]

Several factors influence horsefly activity in the field. They are lovers of sunshine and warm weather. Cool, cloudy and windy conditions limit their movements considerably, and activity practically ceases during rainfall.

During the present work an attempt was made to investigate the effects of each factor and only data showing the influence of a particular factor, when all other factors are favorable for fly activity, have been recorded below. The observations were made at the farms of the University of Massachusetts. The flies were collected from living animals as soon as they had settled, by placing a small wide-mouth bottle over them.

Wind dominates fly activity in the field irrespective of any other factor. Light to gentle wind with an approximate velocity of 4 to 12 miles per hour does not disturb the flies, but with the coming of fresh wind, 19 to 24 miles per hour, the activity decreases (Tables I, II). It was commonly observed that under normal conditions for fly activity, a gust of fresh or strong wind took the flies from the animals, but they appeared again as the wind velocity decreased. Similar effects of wind have been observed by Tashiro and Schwardt (1949).

Light and rain play a significant role. The activity is much less during cloudy weather than under sunny conditions (Table III).

Table I. *Effect of wind movement on tabanid activity (1949)*

	Light to gentle wind	Fresh wind	Strong wind
Number of flies collected in 15 minutes	0,1,9,3,19, 9,23 9,8,8,12,25, 23	3,12	0,1,0
Average	11.46	7.5	0.33

[1] This is a part of a thesis for the doctorate submitted at the University of Massachusetts, and the author wishes to express his sincerest thanks to Professor Harvey L. Sweetman under whose kind direction this work was undertaken.

TABLE II. *Effect of wind movement on tabanid activity (1950); number of flies collected in 15-minute periods*

	T. lasiophthalmus	*T. lineola*	*T. quinquevittatus*
Light to gentle wind	22,7,6,19,14	12,12,18,11,11,13,12	5,5,3,4,9,6,5
Average	13.6	12.7	5.28
Gentle to fresh wind	1,5,3	4,5,2	3
Average	3.00	3.66	3.00
Strong wind	2	—	—
Average	2.00	—	—

TABLE III. *Effect of light conditions on tabanid activity*

T. lineola			*T. quinquevittatus*		
Temperature	No. of flies		Temperature	No. of flies	
	Cloudy days	Sunny days		Cloudy days	Sunny days
25° C	8	12	24.5–25° C	2	5
26–26.5° C	14	12	25.5–26° C	0	5
27° C	7	13	25.5–26° C	3	—
Average	9.66	12.33		1.66	5.00

TABLE IV. *Effect of temperature and relative humidity on tabanid activity with other conditions favorable*

T. lasiophthalmus			*T. lineola*			*T. quinquevittatus*		
Temperature, °C	Relative humidity	Number of flies collected	Temperature, °C	Relative humidity	Number of flies collected	Temperature, °C	Relative humidity	Number of flies collected
20	70	19	20	79	0	20	79	0
22	58	22	22	53	8	22	53	6
28.5	70	7	22.5	55	5	22.5	55	9
29.5	40	6	25	47	12	25	47	5
30.5	66	14	26	57	12	26	61	5
			26	61	4	28	62	5
			27	36	13	28	68	3
			27.5	45.5	12	29	58	4
			28	62	18			
			28	68	11			
			29	58	11			

From field observations it can be safely concluded that fly activity is negligible during rain. No flies were seen in the field between 23° C and 24° C during rain.

The preferred temperature for activity of *T. lineola* lies between 25° and 29° C (Table IV). Activity was negligible at 20° C. No marked response to relative humidity could be obtained. However, the flies were active at the relative humidity existing when the temperature was favourable.

In all probability wind effects, though dominant, are temporary and the fly activity is greatly influenced by some combination of temperature and light conditions.

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SPHERICAL ILLUMINATION AS AN ECOLOGICAL PARAMETER, AND AN IMPROVED INTEGRATOR[1]

Introduction

Light falls on the leaf or stem of a plant from all directions, some directly from the sun, some from the sky, and some after reflection from other objects. It seems clear that any technique of measuring illumination which neglects this simple fact cannot give a result which represents the energy incident on a blade of grass or a pine needle.

Most commercial physical illuminometers measure light falling on a flat surface from a more-or-less extended region, only rarely approaching a complete hemisphere, and in most instances emphasizing the light incident in directions near the normal to the surface. The properties of such an instrument are shown in Figure 1(a), while those of an ideal "spherical illuminometer" are shown in Figure 1(b). In these figures the length of each arrow shows the relative response of the instrument to light arriving from the direction indicated. These figures are not to be considered as a criticism of ordinary illuminometers, many of which are excellently suited to the purposes of illuminating engineering or of photography, but are only intended to emphasize that the quantity measured by the illuminating engineer is not necessarily the best quantity for the plant physiologist or ecologist.

Definition of Spherical Illumination

The concept of spherical illumination is of so little importance to the illuminating engineer that it is not mentioned in Walsh's great work on photometry (1926). It was introduced by Weber (1916) in a paper dealing with the optical properties of the atmosphere, under the name *Raumbeleuchtung* (space-illumination). In order to make the nature of this quantity clear, let us first recall the definition of illumination.

By definition, a point source of I candles radiates I lumens per unit solid angle. Let us imagine a surface S (Fig. 2) of dimensions small in comparison with its distance r from this source, and subtending a solid angle ω at I. Then

$$F = I\omega \text{ [lumens]} \tag{1}$$

will be incident on S. Let θ be the angle between the normal to S and the direction of the light. Then

$$S \cos \theta = \omega r^2 \tag{2}$$

and therefore

$$F = IS \cos \theta / r^2 \text{ [lumens]} \tag{3}$$

The flux per unit area incident on S is

$$E = F/S = I \cos \theta / r^2 \tag{4}$$

E is the illumination produced on S by I. It is expressed in lumens per unit area, for example, lumens per square foot.

Similarly if there are a number of sources of intensity I_n ($n = 1, 2, 3, \ldots k$) when measured in the direction of S, the angle of incidence of the light from each source being θ_n, and its distance r_n, the total illumination on S from all the sources is

$$E = \Sigma_{n=1}^{k} I_n \cos \theta_n / r_n^2 \tag{5}$$

[1] Contribution from the Division of Physics, National Research Council, Ottawa, Canada.

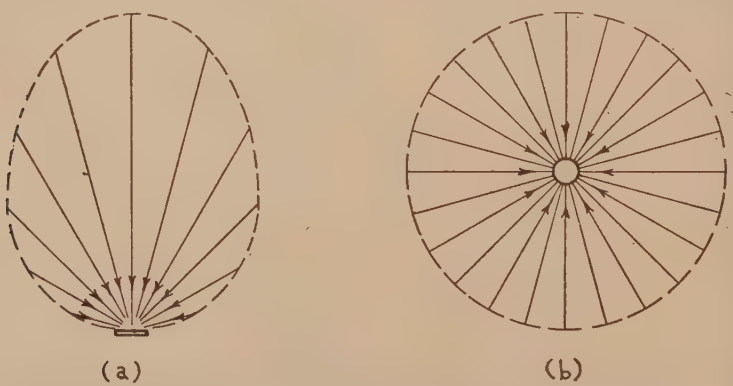

Fig. 1. Relative response of: (a) ordinary illuminometer, (b) ideal spherical illuminometer, to light arriving from different directions.

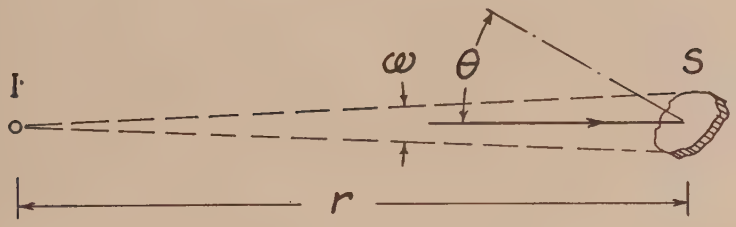

FIG. 2. Calculation of illumination by a point source.

provided that all the sources are on the same side of S.

We may now pass to the case of a continuous distribution of luminance in the hemisphere above S (Fig. 3). Let this luminance be B_θ, in the direction defined by the spherical coordinates (θ, α), $\theta = 0$ referring as before to the normal to S. Then

$$E = \int^{2\pi} B \cos\theta d\omega$$

$$= \int_0^{2\pi}\int_0^{\pi/2} B_{\theta,\alpha} \cos\theta \sin\theta \, d\theta d\alpha \qquad (6)$$

The limits of this integral express the "one-sidedness" of the concept of illumination.

It was to get away from this restriction that the idea of spherical illumination was developed. In the place of the flat element of surface S, let us put a small sphere, the equatorial cross-section of which may for convenience be unity (Fig. 4). This sphere may be thought of as perfectly transparent. Consider an element of the surroundings which subtends a solid angle $d\Omega$ at the center of the sphere and has a luminance B; the flux through the sphere due to $d\Omega$ is then

$$dF = Bd\Omega \qquad (7)$$

and the entire flux in all directions through the sphere is

$$F = \int^{4\pi} Bd\Omega \qquad (8)$$

The spherical illumination is *defined* as this flux through a unit sphere:

$$E_S = \int^{4\pi} Bd\Omega \qquad (9)$$

or in spherical coordinates,

$$E_S = \int_0^{2\pi}\int_0^{\pi} B_{\theta,\alpha} \sin\theta \, d\theta d\alpha \qquad (10)$$

The units are lumens per square foot, etc., as for ordinary illumination.

Note the two differences between equations (6) and (10): the limits of θ, and the absence of the factor $\cos\theta$ in the latter equation.

It is of interest to note that the spherical illumination from uniformly bright surroundings of luminance B candles per square foot is $4\pi B$ lumens per square foot.

The above definition has practical significance, as may be seen by considering the total energy absorbed by a completely absorbing (black) sphere of unit cross-section from its radiating surroundings. This is given by equation (10),

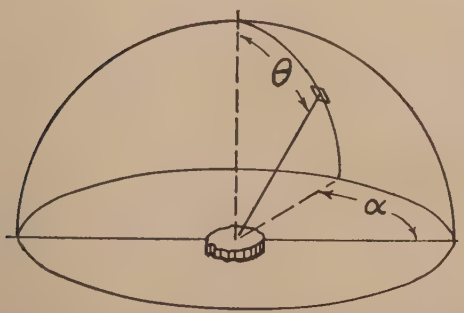

FIG. 3. Calculation of the illumination produced on a plane by a distributed source.

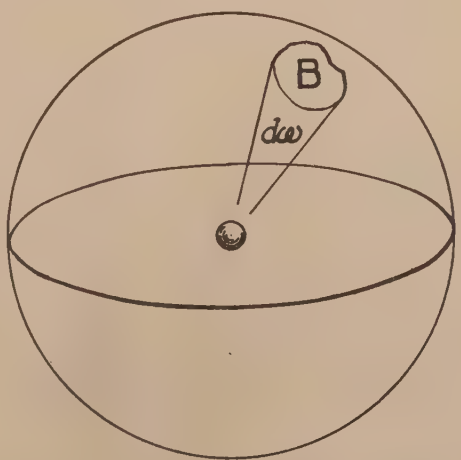

FIG. 4. Illustrating the definition of spherical illumination.

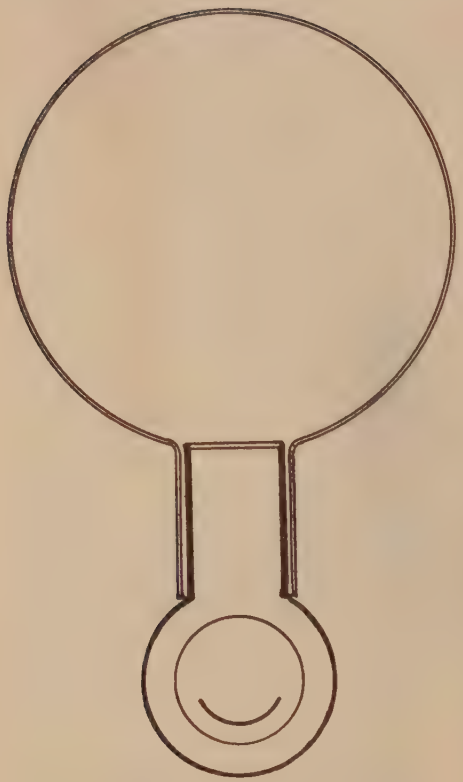

FIG. 5. Fundamental basis of construction of a photoelectric spherical illuminometer.

which might equally well be written in terms of radiation: [2]

$$H_S = \int_0^{2\pi}\int_0^{\pi} N_{\theta,\alpha} \sin\theta \, d\theta d\alpha \text{ [watts/ft}^2\text{]} \quad (11)$$

We might summarize the above discussion as follows: The familiar quantity, illumination, presupposes a flat surface to be illuminated, whether by one or several lights or by the entire sky. Many practical objects, such as the leaves of plants, can receive radiation from all sides. Therefore, as a measure of the radiation received by such objects, a quantity must be defined which is independent of direction. Such a quantity is spherical illumination, which is equal to the entire luminous flux passing in all directions through a sphere of such a size that its equatorial cross-section is of unit area.

[2] The symbols F, E, B, H (irradiance), N (radiance) are those recommended by the Optical Society of America.

Measurement of Spherical Illumination

Spherical illumination can be measured by any receiver having spherical symmetry. A good approximation to such a receiver is a translucent diffusing globe provided with a narrow opaque neck closed at its proximal end by an opal glass disk and carrying a phototube at its distal extremity (Fig. 5). The error due to the presence of the neck is a minimum if it is directed towards the region from which least radiation is coming, and this is the natural and convenient thing to do. Alternatively, the luminance of the opal glass disk can be measured by visual photometry, as was done by Weber (1916), but this necessarily introduces the observer into the vicinity of the photometer.

Integrating Spherical Illumination

For many biological problems, it is desirable to integrate the readings of a spherical illuminometer to obtain the total amount of light (lumen-hours/ft.^{2}) incident on some organism or organ. This may be done by using a recording electrical meter to make a graph of the instantaneous spherical illumination, and then measuring the area under the graph for the period in question. A much neater solution, adequate for many purposes, has been described by Sprague and Williams (1941, 1943). In their instruments, a photo-emissive photocell is employed, the current through which charges a high quality capacitor until the voltage between its plates is sufficient to start the discharge in a special form of glow-tube. This discharges the capacitor and also operates a counter. Assuming a linear relationship between photo-current and spherical illumination, each count represents a certain definite amount of light incident on the photometer.

An Improved Integrating Spherical Illuminometer

The instrument to be described here was designed at the request of the Forest Research Division, Forestry Branch, Department of Resources and Development. It is exactly similar in principle to the second one described by Sprague and Williams (1943), but has certain improvements in design. In the main these are:

(a) A superior mechanical design, in which the sensitive parts of the electrical circuit are completely protected from moisture by a very strong container;

(b) An improved shape, leading to a more nearly complete spherical symmetry of response to incident light;

(c) A spectral sensitivity very like that of the normal human eye (any other reasonable distribution of sensitivity could be obtained by substituting the proper filters);

(d) A range-changing switch, operable from outside the instrument.

The construction of the illuminometer may be explained by reference to Figure 6 which presents an axial cross-section of the instrument. All the working parts are housed in a sturdy brass case composed of several turned pieces and a brass tube. The joints which can be permanently connected are soldered and those which have to be broken from time to time are made water-tight by rubber "O"-rings. For the mechanical design of this exterior part of the instrument, the writer is indebted to Mr. George Klein of the Division of Mechanical Engineering.

Projecting from the top of the instrument is the opal glass bulb 4″ in diameter on which falls the light to be measured. The surface of this sphere is completed by an opal glass plate carried at the end of a brass tube 2″ long. At the other end of this tube are found the necessary light filters to correct the No. 926 phototube to the approximate spectral sensitivity of the normal eye. A second opal glass plate, mounted on three thin strips at a distance of 1¼″ above the other, greatly improves the directional response (see below).

Below the photo-tube are mounted a trigger tube No. 313C and two capacitors, one having about 10 times the capacitance of the other. A lever projecting from the bottom of the instrument makes it possible to switch in one or both of the capacitors. In the space between the trigger tube and the photocell is packed a small bag of silica gel which keeps the inside of the instrument quite dry. This is necessary

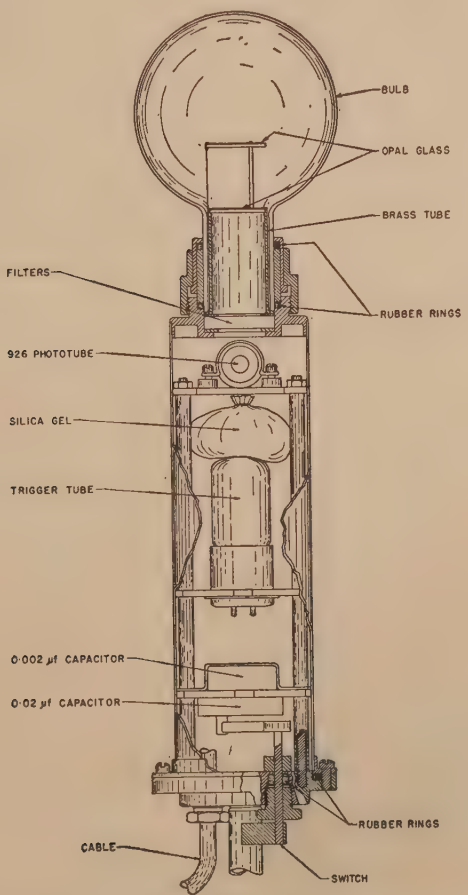

FIG. 6. Cutaway view of the new spherical illuminometer, showing all the working parts. The wiring is omitted in the interests of clarity.

if the calibration is to be accurately maintained. The base of the instrument is threaded for a ⅜" standard iron pipe and in the ordinary use of the instrument outdoors this is merely stuck into the ground.

Connections to the remainder of the apparatus are made by means of a three-wire shielded cable of very high quality.

The electrical circuit is shown in Figure 7. In this figure, the parts inside the instrument are enclosed by a dashed line while the remaining parts comprising batteries, a resistor, a two-microfarad capacitor, and a counter are at the other end of the cable. The counter is a small instrument made by the Cyclotron Specialties Company and operates on a few milliamperes.

All the electrical parts are of the highest quality. The small capacitors inside the instrument are mica condensers and the two-microfarad capacitor is a high-quality, oil-filled paper condenser in a metal case. The batteries are ordinary 45 volt blocks of medium size and last two or three months in ordinary service.

Mode of Operation

The operation of the illuminometer is simple. Light falling on the photocell causes it to pass a small current. This gradually charges up one or both of the capacitors in the instrument (depending upon the position of the switch) and thus the potential of the starting electrode of the trigger tube gradually rises. When this reaches a definite value it starts a discharge through the trigger tube. The energy for this discharge is supplied by the two-microfarad capacitor which has already been charged to the full voltage of the battery. In this manner, a pulse of current is sent through the counter. At the same time, the small capacitor is discharged completely and its charging by the photo-current can recommence. The resistance in series with the battery and the large capicitor is so adjusted that the large capacitor will be fully charged in rather less time than the small capacitor is charged at the maximum illumination it is desired to measure. There is a minimum usable value for this resistance because if it is too low, the discharge through the trigger tube will be maintained by the battery.

Since the photo-current is very nearly proportional to the amount of luminous energy falling on the photo-tube per unit of time, each count represents a certain definite amount of luminous energy per unit of area. The calibration is given in terms of lumen-hours per ft.^{2} for each count.

The ultimate sensitivity of a circuit of this kind is determined by the dark current through the photo-tube. This varies from one instrument to another, but should not be more than about 15 counts per hour with good construction and a selected photo-tube. It may be only

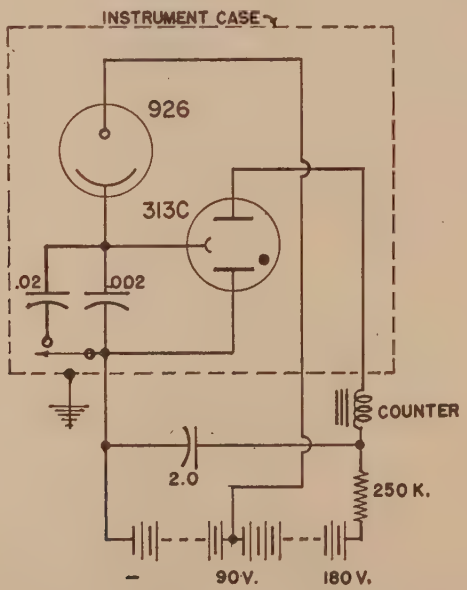

Fig. 7. Electrical connections. The components outside the broken line can be located at any reasonable distance from the illuminometer.

one or two counts per hour, but in case it is appreciable, the appropriate number of counts must be subtracted before the reading of the instrument is converted into lumen-hours per square foot.

Calibration of the Spherical Illuminometer

It was hoped that the response of the illuminometer would be almost entirely independent of the direction of the incident light except from directions near the body of the instrument. This uniformity depends on the uniformity and diffusing qualities of the bulb. It was tested by measuring the response to a uniform beam of collimated light directed at the illuminometer from various angles. Without the second opal glass plate mentioned above a nearly parallel beam incident axially was found to give about 18 per cent greater response than the same illumination incident at right angles to the axis of the illuminometer, but the additional plate reduces this difference to a point where it is masked by small non-uniformities in the lateral response. These amount to about $\pm$ 5 per cent. It may thus be concluded that the instrument is reasonably satisfactory in this respect.

To perform the actual calibration of the illuminometer, it was placed in a large integrating sphere 12 feet in diameter, incandescent lamps of various sizes being placed one at a time in the sphere with it to give different amounts of illumination. The illuminometer was shielded from the direct light of the lamp by a circular white screen. Because of the intrinsic properties of the integrating sphere, the surroundings of the illuminometer are of uniform luminance in all directions. This means that B in equation (9) is a constant so that the spherical illumination is simply $4\pi B$.

This calibration was made at a color temperature in the vicinity of about 2800° K. Since this is much yellower than sunlight or light from the sky, the adequacy of the light filters in the instrument was checked by measuring the transmission of a blue filter used for converting light at 2850° K to about 6500° K. This measurement gave a satisfactory agreement with the transmittance calculated by spectrophotometry.

Performance

During the summers of 1951 and 1952, two of these illuminometers were operated at the Forest Research Station of the Department of Resources and Development, Petawawa, Ontario. Practically no trouble was experienced with the instruments. When they were brought back for recalibration during the winter of 1951–52, it was found that the silica gel was not at all moist, indicating that the cases had remained hermetically sealed and that no moisture had entered during the entire period. The dark current in one instrument had actually decreased considerably and in the other it had remained negligible. The recalibration agreed with the original one to within 10 per cent. During the summer of 1951, the instruments were without the range-changing switch and had only one capacitor. Full sunlight was outside their range and the second capacitor and the switch have since been installed to enable the range to be changed at will. It is not possible to make the instrument operate at more than about two counts per second because the large external capacitor cannot be charged rapidly enough without maintaining the discharge in the trigger tube. It will be noted that the switch is placed inside the instrument case. If it were placed at the other end of the cable, the insulation resistance of the cable would enter into the calibration of the instrument with a possibility of large errors due to changing humidity. If it were essential to change the range from a distant point, a small relay could undoubtedly be built into the illuminometer.

Acknowledgments

In addition to the invaluable help received from Mr. George Klein of the Division of Mechanical Engineering with the mechanical design, the writer wishes to acknowledge the continued cooperation of Mr. J. L. Farrar and Mr. K. T. Logan of the Forest Experiment Station who used the instruments during the summers of 1951 and 1952. Finally, he wishes to thank his colleague, Mr. C. L. Sanders, for his careful calibration of the instruments.

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AN EXPERIMENTAL APPROACH TO THE STUDY OF PLANT AND ANIMAL REPRODUCTIVITY AND POPULATION WITH A LIFE SCIENCE BUILDING PLAN

The size of seed crops and the size and vigor of animal populations have been matters of year-to-year concern of the human race from the earliest times. Likewise the number and vigor of disease-producing organisms have periodically caused apprehension. In attempting to meet the problems arising from these challenges to human existence, the role of fecundity and vigor of offspring has not received adequate attention. However, in the past quarter-century correlations of populations, seed crops, etc. with physical and biological factors have been recorded, but experimental effort has been limited, both in the plant and the animal fields.

If sound generalizations are to be attained and further progress made, experimental work must analyze and check interpretations of observed natural biological phenomena. Experiments are in the same way especially important when management or control of wild species is involved. In this case incorrect methods may result in much waste of funds and effort.

Although technology has brought under control most of the commonly recognized factors, control of radiant energy remains an outstanding difficulty in experimental work principally because of poor building plans which usually make it impossible for the investigator to control the impact of sunlight or to utilize out-of-door facilities. When an investigator departs from the use of organisms of the fungus, cockroach, or white rat types he encounters the problem of keeping the organism alive and normal while under experimental treatment. The plan in Figure 1 is presented to show a means of bringing natural environmental factors under control and measurement. The plan will permit physiological and ecological studies to be conducted under (1) measured natural conditions and (2) controlled laboratory conditions as well.

Figure 1 shows the proposed arrangement of a laboratory building. It is on a lot 500 ft. square inside of sidewalks. The main building is 400 ft. long, facing north, with back yard 300×450 ft. surrounded by one-story buildings completely enclosing the yard. Interest in the main building is incidental as it is merely so arranged as not to interfere with the essential features to the south of it. The ends of the southward-projecting wings are on the shadow line of the sun as it rises over a 70-foot obstruction at 6 a.m. June 21 at Latitude 40° N. On the east and west, the 70-foot obstruction must be approximately 90 feet outside the limit of the one story building. At the south this distance is 85 feet, fixed by winter positions of the sun. This arrangement gives an area 170 feet by 200 feet on which there are no shadows from 6 a.m. to 6 p.m. throughout the year. Its total possible sunshine has been calculated, and a table covering sunlight at 40° N, ultraviolet intensity, etc. is available (Shelford 1951).

As to the suggested one story buildings, the small glass-roofed buildings at the center are primarily for research (Went 1950) and are separated so that the roof condition of one will not interfere with the others. The long greenhouse is for general plant work. The two lateral glass roofed areas, one for plants and one for animals, have lighting up to the standards of average college greenhouses.

The normal activities of three or more instructors (investigators noted under 1 to 9 below) together with the necessary field and experimental equipment etc. call for at least 50,000 to 60,000 cubic feet of storage space, which, along with a considerable part of the animal space, need not be heated.

The three reasons for some of these facilities constituting a complete wall around the out-of-doors space are : (a) the public is inclined to assume that caged animals are being or have been tortured, and certain organizations have caused much trouble and embarrassment for investigators on this basis. (b) Such areas within reach of streets and protected only by fences and shrubbery receive lighted cigarettes which cause fires, and much trash, cans, bottles, etc. This is especially true of ponds. Ducks, for example, are likely to be fed by the public through a fence. (c) All experiments must be protected from interference by unauthorized persons.

Researches based upon analyses of population and seed crops in relation to weather and solar radiation have led to conclusions requiring experimental confirmation in facilities such as are described. Additional problems and results are enumerated below in relation to the facilities proposed.

1. Glass-Roofed Space; Plant-Animal Relations; Plant Demonstrations.

The need for glass-roofed space for plants for instruction and research can hardly be denied. A few institutions have greenhouses the equivalent of the long one (Fig. 1) for general purposes. The need for glass-roofed space for studies of plant-eating insects is suggested by the fact that fecundity of the chinch bug, a crop pest, is influenced by the salts used

in the plant culture solutions and by differences in the food plants. Dahms (1947) and Dahms *et al.* (1936) found that there are sharp differences in the number of eggs laid by female chinch bugs fed on 10 species and varieties of plants of the grass family. The number of eggs varied from 1378 on Johnson grass, *Sorghum halepense,* to none on a variety of *Sorghum vulgare.* The development of chinch bug nymphs is more rapid and the mortality less on milo sorghum than on atlas sorghum. An example of a study requiring outdoor space is that of Painter and Jones (1948) who found that the resistance of Pawnee wheat to Hessian fly is due to the fact that the majority of larvae which reach the feeding position on the plant fail to grow and mature.

2. Dark Rooms and Photoperiodism (Garner and Allard 1920).

Different lengths of periods of daylight control the initiation and success of reproductive phenomena in many plants and animals, especially flowering plants and the higher vertebrates. In the very large insect group, aphids alone appear to have been investigated (Marcovitch 1924), and bulls were shown to be affected by Mercier and Salisbury (1947). Bissonnette (1938) summarized the work on birds and mammals, much of which was experimental, and later showed photoperiodic changes in the quality of the pelt of the weasel (requires protection or management) (Bissonnette and Bailey 1944). An examination of the literature which he cites indicates that most

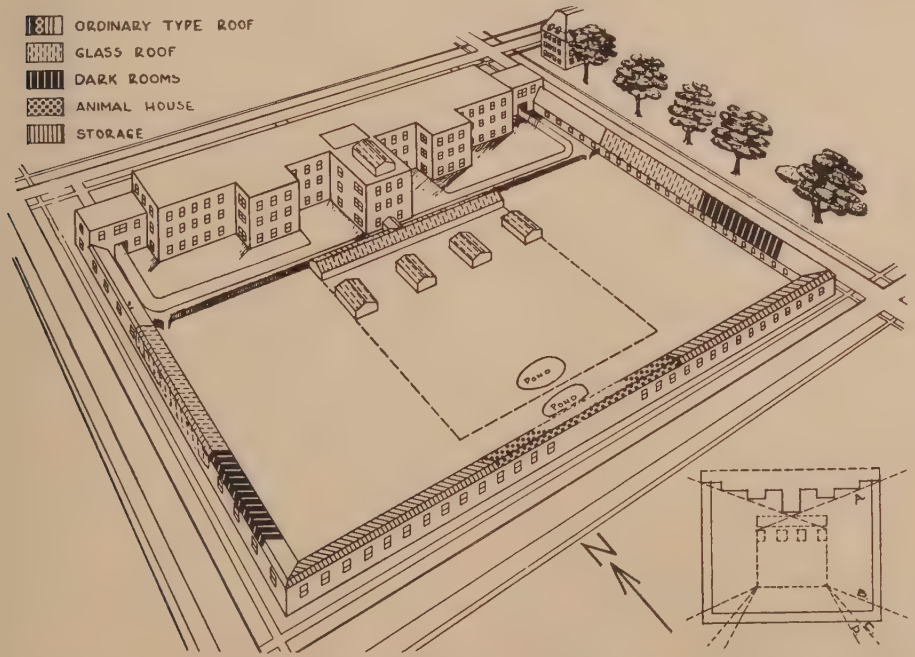

FIG. 1. As drawn the one-story building is connected with the main building by a 50 ft. length of two story structure to provide vehicular entrance. The height of the roof of the one-story building is suggested to be 17 ft. at the peak, with the peak being much nearer the outer wall than the inner to meet the shadow limits. For the sections on the east and west sides of the yard, an overall width of 25 ft. is suggested for the one-story building with rooms 17 ft. wide and a 5.5 ft. arcade along the inner side. The service tunnel should be below the arcade along the inner side so that all service pipes may enter spaces in which vertebrate animals are present, through the side walls. The various roof shadings indicate the type of rooms beneath. The northernmost portions of the one-story structure could be designated as space for the investigators using the facilities farther south. The one-story section which bounds the yard at the south needs be only 15 to 18 ft. wide and unheated. A considerable portion may be of cage construction and only half roofed, for native animals. The angles of the sun at various times are shown in the inset: A, June 21, 6 a.m., 70°; B, March or September 21, 8 a.m., 110.4°; C, December 21, 9 a.m., 137.7°; D, December 21, 10 a.m., 150.2°.

of the important results have been achieved under difficulties in courts, basements, barns, etc. without equipment for accurate measurements.

In the field of plant science the most striking findings are contributions to the knowledge of the hormone mechanisms recently discussed by Leopold (1951) and of the sensitive or critical periods in plants (Hammer 1948, p. 115) which should be studied in the important wild plants. The internal phenomena and the effects of photoperiodism on wild plants are barely touched (Olmstead 1945) and this whole field which is so important to the solution of the problems of the ecologist, geographer and palaeontologist remains largely to be explored.

As a common practice in work on photoperiodism, plants are grown in pots and drawn into a dark room from an open area on trucks, to give any length of day desired. The same method can be used for animals, including plant-eating insects—a relatively unexplored group. In the case of the large ones almost no other method is readily available.

3. Known Sun Exposure, Light Intensity and Duration of Intensity.

Some plants and animals require shade or partial shade. Plant relations to light are well known (Corbett 1899; Shirley 1935). Such animal studies are few but there are some correlations. This author's unpublished work indicates that the population increases of the plains antelope and prairie chickens give indications that the percentage of possible sunshine of the preceding mating season is important. Some of the hormones in animals, the production of which largely controls fecundity, are definitely related to light. They have been discussed by Whetham (1933).

4. Populations of Animals and Reproduction of Plants in Relation to Ultraviolet Light. (See Pettit 1924-1938 and Stetson 1947.)

Two long population records, one for the chinch bug and one for the quail (Errington 1945), show correlations with solar ultraviolet intensity (Shelford 1951) of a pre-breeding period of approximately a month. This correlation is with reference to an optimum. Increases occurred in both species when April ultraviolet was within the optimum range; decreases came both when the intensity rose above the optimum and when it fell below the optimum. In the case of the cottontail rabbit the condition of the testes is known histologically (Ecke 1948). The month of February is the period of germ-cell development and the month before actual mating. February ultraviolet was used for suggesting a possible basis for the interpretation of population increases and decreases (Shelford 1951).

The importance of short-wave radiation is indicated by (a) induced increase in egg production in poultry (Bailey 1950), (b) shortened period to oestrus in the ferret (Marshall and Bowden 1934), and (c) initiated reproduction of a grouse locust (Sabrosky, Larson and Nabours 1933). All these results have been brought about by long exposure to weak violet and near ultraviolet light. These studies are of critical significance. In the case of the grouse locust, Sabrosky *et al.* produced the result with a light at 24 inches for about two months, thus following the indication in nature. Steen (1933) secured detrimental results in *Drosophila* with short exposures to a similar light at 9 inches, giving 13 times the intensity used on the grouse locusts. (See also Arthur and Hawill, 1947)

5. Sensitive Periods in Life Histories, Master Factors and Environmental Variability.

In the life histories of annual organisms and in the annual cycles of organisms with relatively long lives, there are usually a number of short, sensitive periods. A good illustration could be drawn from the annual cycle of an oak tree with variable acorn crop, but the peach tree is used because detailed information is not available for an oak. Each year a peach tree is most sensitive to low temperatures in a period of about ten days from the opening of the blossom to the dropping of the calyx tube. If the temperature falls to 24° F or even 27° F under certain conditions the young fruits are killed and the fruit and seed crop destroyed (personal communication from M. J. Dorsey). Larsen (1943) would call low temperature a master factor. Master factors control an entire operation essential to the life of the individual or the species.

Well-known domestic animals have such sensitive periods also. In the absence of studies of wild species the sheep in England can be cited. Johnson (1926) discussed critical periods for sheep and pointed out that the rutting season and lambing season fall within narrow limits of temperature, rainfall, and humidity. His results are based upon long records of success and failure in the industry. (See also Tehon (1945) on plant diseases.)

Various types of variability of temperature and humidity, etc. are very significant. Constant temperature slows insect development from 2 to 10 percent in various species. Went (1950) pointed out six temperatures fitting into six sensitive periods of the hyacinth life cycle. He further pointed out there is a growth optimum for day temperatures and a corresponding growth optimum for night temperature in the tomato plant.

6. Bioclimatology.

A few institutions are now giving courses in bioclimatology of mammals which are concerned with the responses to variations in the environmental factors and the application of

meteorological and climatological techniques to physiological studies of man. These courses are the outgrowth of studies made in the army where out-of-doors conditions could be used.

7. Animal Parasitology.

This kind of work calls for out-of-door cages for dog-sized animals. *Diphyllobothrium* sp., tapeworms from fish-eating birds, are considered by British workers as probable parasites of man but there is no experimental proof. Thomas (26) has completed one of these bird tapeworm cycles and is now engaged in determining whether or not they will infect man or other mammals with detrimental results. Outdoor cages for wild mammals and birds and also ponds are absolutely necessary for this checking.

8. Ornithological Studies.

Studies of birds often require out-of-door cages and concrete pens. The enclosed yard is a suitable place for trapping song birds.

9. Ichthyological Studies.

These are concerned with life histories, rate of growth, etc. which call for good water and both inside and outside aquatic facilities, the former mainly under glass.

Summary

About 5,000 teachers, investigators, and especially postgraduate students in the United States in the fields of plant ecology and taxonomy, wildlife, ornithology, animal ecology and ichthyology are deprived of opportunities to do experimental work because of obsolete campus and building plans. Their students go out inadequately prepared. The interpretation of natural biological phenomena is retarded, geological interpretation of the past impaired, and many practical problems remain unresolved. There is in all probability as good a chance of outstanding discoveries in these fields as elsewhere. All the knowledge and facilities of biophysics and biochemistry will be required to analyze the basic phenomena.

The plan suggested is not intended to minimize the importance of other laboratory research carried on in such a life science building. However, because the research and instruction described above require facilities which do not readily fit into the conventional architectural plans it is important that such facilities be adequately described and made available.

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THE EDAPHIC FACTOR IN PLANT ECOLOGY WITH A SPECIAL NOTE ON SOIL PHOSPHATES[1]

During the past few years, ecologists have recognized the importance of soils in plant ecology. However, in spite of this recognition and the fact that agriculturalists have published a wealth of information on the effect of soil properties on crops, few attempts have been made by ecologists to apply these now well-established agricultural principles to natural vegetation. Indeed, much has been published in ecological literature on soil properties and on the processes of soil formation, to the exclusion of the effects of the individual soil properties on vegetation. There are a few notable exceptions; for example, the concentration of salt, soil pH, soil water.

Soil properties can affect vegetation in two ways: firstly, by controlling the floristics, and secondly by controlling structure. Floristic composition is controlled by the selection of species suitable to the area. Selection may occur at the germination stage or, more frequently, in the early stages of the seedling, or even at the near-maturity stage through competition. On the other hand, community structure is determined partly by the habit of the species that succeed in the area, partly by the relative levels of the various plant nutrients (including water), which determine the size attained by the individual plants, and partly by the manner in which the various species have become adapted to the limited factor of the environment. Before a discussion of these statements is attempted, it will be necessary to comment on the usage of the term "edaphic factor."

Discussion of the Edaphic Factor

Until Major's paper was published (1951), ecologists used freely the term "edaphic factor" as one of the variables affecting vegetation, usually with the full realization that this factor is strictly dependent and that soil and vegetation are interdependent. Major's contention that "soil parent material factor" should be substituted for "edaphic factor" challenges this established custom; he naturally and justifiably calls for a critical examination of the basic principles. Major's criticism of the edaphic factor as opposed to the soil parent material factor is founded on the distinction between dependency and independency of the factors; thus soil parent material being independent is preferred to soil which is dependent.

In the writer's opinion, the criterion of dependency or independency of the several vari-

[1] The author is indebted to Drs. J. McLuckie and H. S. McKee for criticism of the manuscript.

ables is of little consequence with regard to the understanding of the factors governing or limiting a plant or a community. Indeed in the most critical diagnosis of the factors affecting and limiting plant distributions and plant communities, the ecologist achieves the most satisfactory results by a consideration of the various parts of the factors which make up the environment. Thus, when soil is the limitting factor, one is concerned not so much with the many soil properties and other environmental factors, but rather with the individual soil property which is imposing the limitation on the system.

The limiting soil property is sometimes a function of the parent material; on the other hand, it frequently is not. For example, three soil properties that commonly govern plant communities both floristically and structurally are

a) The concentration of NaCl,
b) Clay pans in the B horizon,
c) Phosphate content.

The first of these is frequently a direct function of physiography and usually is not related in any way to soil parent material. The second develops by the interaction of the various factors of the environment, and in certain cases is controlled by rainfall rather than by parent material. The third is frequently a direct function of parent material.

Further relevant observations that may be used in defense of the retention of the term "edaphic factor" are given by the relative selecting values of the parent material and soil during a succession. For example, if two successions on two quite different parent materials are traced (*e.g.* limestone and granite), it becomes apparent that the effect of the parent material diminishes with time. Whereas the primary colonizers (microorganisms, lichens, and mosses) are selected by the parent material (because the chemical properties of the parent material dominate the environment), later stages in the succession are selected by soil properties. Consequently, two parent materials as unlike chemically as limestone and granite may produce approximately the same climax vegetation, because this climax is controlled by a certain soil property which develops in both soils as a result of the interactions of the various environmental factors on two different parent materials.

In the light of these considerations, the writer considers it preferable to retain the term "edaphic factor" on the grounds that this term may be used in a collective sense to refer to the many soil properties which may control the vegetation. Its replacement by the term "soil parent material factor" would over-emphasize the importance of one soil-forming factor Jenny 1942) and, perhaps, fail to isolate the soil property which is controlling the vegetation.

Soil Nutrients as Limiting Factors

In theory, any one of the essential elements obtained from the soil may be a limiting factor. For example, Billings (1950), working in Nevada, U. S. A., found that differences in the amount of available nutrients can determine both structure and floristic composition. His figures indicate that, for his specific example, soil phosphate is in lowest supply. A similar condition has been recorded in Australia by the writer: the results of extensive investigations on soil nutrients, and chemical analyses of the leaves of plants (data unpublished) lead to the following conclusions, which confirm those made by Billings. Under Australian conditions, the elements required in the greatest quantity by the plants (fixed nitrogen and phosphate) are the first to become limiting.

The result of a low nutrient supply is firstly the selection of the flora. Thus, plants that have become adapted to low nutrient levels are capable of surviving in the low nutrient media, while those with higher requirements are excluded. Also the structure of the community is affected since the size of mature plants is affected by the limiting soil nutrient. Consequently, in areas of uniform climate and physiography distinct patterns of vegetation develop, which are determined by the concentration of the limiting nutrient.

It is sometimes possible to correlate the mineral deficiency with the various factors of the environment, *e.g.*, the parent material may be deficient in the element in question, or possibly the deficiency may arise through extreme leaching of the soil or by chemical fixation. Evidence that the former is common is supplied by analyses and experimentation (see below). On the other hand, no proof that soil leaching is directly responsible has yet been recorded by the writer, while the available data on the concentration of nutrients in drainage waters would suggest that this condition is uncommon. Furthermore, it appears most probable that mineral nutrients are retained so avidly by the soil-plant system that little escapes; this is undoubtedly true for the communities growing on infertile soils around Sydney (Beadle and Burges 1950).

It is well-known among agriculturalists that Australian soils have a very low phosphate content. In the Sydney district, at least, phosphates play the greatest rôle in determing vegetation patterns. Thus, the scrubs, dry sclerophyll forests, and wet sclerophyll forests are delimited by soil phosphate. In this case, the phosphate content of the soil is directly governed by the soil parent material. The low level of phos-

phate has two important effects; firstly, it limits the growth of green plants; secondly, it limits the growth of nitrogen-fixing organisms (especially the non-symbiotic) so that the level of soil nitrogen also is extremely low. Pot experiments using flax grown from seed as a test plant in the green house to ascertain the various nutrient levels of the various soils provide the following quantitative data. For the most infertile soils, which suport scrubs and low stands of dry sclerophyll forest, flax plants produce only cotyledons and 3 or 4 pairs of mature leaves after a period of six weeks. When phosphate alone or nitrate alone is added, the plants grow to approximately the same size as the unfertilized plants. When both phosphate and nitrate are added, robust plants bearing some 15 pairs of mature leaves are produced. On the other hand, unfertilized soils from less xeromorphic communities (*e.g.* wet sclerophyll forest) produce flax plants larger than the poorest soils but not as large as the phosphate plus nitrate treatment, whereas unfertilized soils from the mesomorphic rainforest produce plants as large as the phosphate plus nitrate treatment. Further to this, an analysis of the leaves of the plants from the various communities shows that the phosphate content of the leaves increases with increasing mesomorphism.

It may be mentioned here as a preliminary note, that fertilizer experiments on potted plants suggest that the degree of xeromorphism of the leaves of some plants, at least, is determined by the supply of phosphate and nitrate. Leaves of certain species (particularly members of the Myrtaceae) can be made to increase enormously in size so that they resemble in texture the leaves of rainforest plants by the addition of these nutrients. Details of this aspect of the work, including the effects of soil phosphate on nitrogen fixation, and the role of phosphate and fixed nitrogen on the degree of xeromorphism will be published at a later date when the experiments in progress have been completed.

A second significant effect of the low nutrient conditions is on the life-form spectrum of the communities. Botanists have frequently commented on the variety of perennials on the sandstone soils and the paucity of non-rhizomateous herbs. A closer investigation of the position reveals that there are no native annual species on these soils (with the possible exception of a few quite rare and very small caespitose monocotyledons, and possibly a few small dicotyledons which are confined to the better soils of the valleys). The explanation appears to be that annuals are excluded because the nutrient levels of the soils are so low that an annual plant cannot obtain sufficient nutrients in a small period of time to survive from year to year. For the same reason introduced annuals which become noxious garden weeds cannot invade the sandstone soils. Pot experiments have proved this point: four noxious weed species (*Amaranthus viridis* L., *Euphorbia peplus* L., *Bidens pilosus* L., and *Setaria glauca* Beauv.) were grown in the greenhouse under optimum climatic conditions in watered but otherwise untreated soils. In no case did the plants produce more than 4 dwarfed leaves, while no plants showed any signs of flowering.

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Craspedacusta sowerbii in Pymatuning Reservoir

Craspedacusta sowerbii Lankester is an organism whose spontaneous and sporadic occurrence makes it unique in the annals of natural history. The records of its occurrence almost lend credence to the ancient theories of spontaneous generation, so unpredictable is its appearance. The freshwater medusa has usually been reported from restricted aquatic habitats, such as aquaria, ditches or small ponds. However, Deevey and Brooks (1943) observed specimens of Craspedacusta in a lake covering an area of 271 acres.

On July 22, 1950, several freshwater medusae were seen by C. A. Tryon, Jr. and myself during the process of routine plankton sampling in the Middle Lake of the Pymatuning Reservoir, near Linesville, Pennsylvania. One specimen was secured and kept alive in an aquarium for four days. This was a male, 12 mm in diameter. It was collected approximately one-half mile from shore in open water of a reservoir covering 13,000 acres, with a maximum depth of 22 feet (Tryon and Jackson 1952). Collection was made in extremely calm

water on a hot, sunny day, but two days previously the lake had been agitated violently by storms. This is the first record of the occurrence of Craspedacusta in Pymatuning Reservoir. It is significant in that the reservoir represents the largest surface area from which the freshwater medusa has been reported. The largest body of water from which Craspedacusta has been reported previously is Lake Wallenpaupack, near Scranton, Pennsylvania, covering a surface area of 6,200 acres (Dexter, Surrarer, and Davis 1949).

A freshwater medusa was collected in the Lower Lake of Pymatuning Reservoir late in July, 1952, by Ralph Ferris. This specimen was brought for identification to the Pymatuning Laboratory of the University of Pittsburgh and proved to be *Craspedacusta sowerbii*.

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ON THE SOUTHERN LIMITS OF THE INTERTIDAL BARNACLE *BALANUS BALANOIDES*

To those interested in the geographical distribution of the littoral barnacle, *Balanus balanoides* (Linn.), the report of its occurrence by Ricketts and Calvin (1939) at Monterey (Latitude 36° 20′ N) is of considerable importance: small specimens (often under ¼ inch in diameter) were said to occur in the splash zone of the pier piles. Previously the most southerly record was at Sitka (Latitude 56° 50′ N)—see Pilsbry (1916). Broch (1924, 1936) considers that *B. balanoides* is a boreal species with sporadic occurrence in boreo-arctic and arctic waters. Hutchins (1947) in discussing temperature zonation and geographical distribution suggests that from the available evidence *B. balanoides* exemplifies what he has termed his Type 2 zonation where the zonal boundaries are determined by the temperature required for repopulation, in this case the summer temperature towards the poles and the winter temperatures towards the equator. The group of limits is approximated by the minimum monthly mean of 45° F (7.2° C); this is in marked contrast to the conditions at Monterey, where the monthly mean for the coldest winter month ranged from 10.2 to 12.6° C and averaged 11.1° C over a 23-year period.

The Monterey record has been referred to, although questioned, by Henry (1942) and it would seem desirable to have material from this region examined again since, with the exception of the record from Monterey, it has not been shown to extend beyond the Aleutian province of Schenck and Keen (1936).

I have been able, through the courtesy of D. P. Abbott of the Hopkins Marine Station who made the collections, to examine a considerable quantity of material from the Monterey wharves. Representative collections were made from the splash zone, the upper zone and the *Mytilus* zone on the Monterey wharves as well as from the upper rocks near the Hopkins Marine Station, Pacific Grove. In all, many hundreds of barnacles have been examined.

No *Balanus balanoides* were found.

The dominant barnacle in all the collections was *B. glandula* Darwin; in the upper zone the individuals were small and regularly shaped, apparently due to lack of crowding; in the lower zones they were present in dense masses both on one another and on other organisms and often resembled very closely the clusters figured by Pilsbry (1916, p. 121, Fig. 7 F). Amongst the *B. glandula* and common in the upper zones were small specimens of *Chthamalus dalli* Pilsbry. In the lower zone was a large (6 cm rostrocarinal diameter) *Balanus aquila* Pilsbry (a species not mentioned by Ricketts and Calvin) covered with closely packed *B. glandula*.

It has been possible, more recently, through the courtesy of Dr. Chace of the United States National Museum, to examine the original material. All that remains are a small number of disarticulated compartments, apparently from more than one specimen. The compartments are all corroded but it is estimated that they have come from barnacles 2–10 mm in height. In the absence of opercular valves and soft parts identification must rest on the compartments. The presence of a calcareous basis would readily distinguish *B. glandula* from *B. balanoides*, but the basis is thin in this former species and is often left behind by collectors. The inside of the parietes is smooth above and quite strongly ribbed near the base; the sheath

is quite hollow at its lower edge. These two characters seem sufficient to identify the material as *B. glandula* since in *B. balanoides* the lower part of the inner face may have low irregular or branching ridges but no ribs and the lower edge of the sheath is rarely hollow beneath (see Darwin 1854 and Pilsbry 1916).

All the evidence then points to the fact that *B. balanoides*, in accordance with earlier observations, does not extend as far south as California.

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ON SOCIAL SINGLE SPECIES POPULATIONS

In all formal mathematical theories of population growth, population increase is considered to be limited by some function of the number of animals present. The classical Verhulst-Pearl equation of population growth can be written as:

$$\frac{dN}{dt} = rN\frac{(K - aN)}{K}, \qquad (1)$$

where N is the number of organisms in the population, r the intrinsic rate of increase and K the size (in one sense) of the available universe. a is a proportionality constant.

Measuring the environment in terms of the number of organisms in the population implicitly assumes that there is something (x) in the environment such that $\frac{a}{K}$ of x is required by each animal at equilibrium. If the total available quantity of x increases in the environment the equilibrium number of organisms in the population increases proportionally.

In effect, the amount of x required by each organism in the population is independent of the other organisms in the population while the amount of x available to each organism is dependent on the total amount available in the environment and on the number of organisms competing for it.

This relation is diagrammed in Figure 2a where the I_i represent individual animals of the population, x the amount of material in the environment, and the pairs of arrows represent the demands of the individuals on the total quantity of x and the amount of x which each individual actually obtains.

The Verhulst-Pearl population equation has been amplified to include two species and the competitive interaction between them (Gause 1935).

Hutchinson (1947) has suggested that certain species-competition situations can be adequately described only by assuming a social interaction between members of each species. This situation is formulated as:

$$\left.\begin{aligned}\frac{dN_1}{dt} &= r_1N_1\frac{(K_1 - a_1N_1 - \gamma N_2^2)}{K_1}\\ \frac{dN_2}{dt} &= r_2N_2\frac{(K_2 - a_2N_2 - \delta N_1^2)}{K_2}\end{aligned}\right\} \qquad (2)$$

where the subscripts 1 and 2 refer to species one and two respectively. K, N, and r retain their previous definition.

γN_2^2 and δN_1^2 express the depressing effect of each species on the population of the competing species. The effectiveness of each species in its interaction with the competing species is directly proportional to the interaction between the individuals of the species.

This is a simple type of social interaction. Hutchinson points out that this is a simple example of a more general case in which γN_2^2 and δN_1^2 are replaced by the power series:

$$\left.\begin{aligned}&\alpha N_2, \quad \gamma N_2^2, \cdots\\ &\beta N_1, \quad \delta N_1^2, \cdots\end{aligned}\right\} \qquad (3)$$

Some interesting conclusions can be derived if a similar notation is used to describe social interactions in single-species population growth.

Consider the case:

$$\frac{dN}{dt} = rN\frac{(K - bN^2)}{K}. \qquad (4)$$

In the initial non-social case (1), the relation between size of the environment (measured as amount of x) and number of animals at the upper asymptote could be written as:

$$K - aN = 0 \qquad (5)$$

while in the simple social case (4), it becomes:

$$K - bN^2 = 0 \qquad (6)$$

while in the most general case it becomes:

$$K - f(N) = 0 \qquad (7)$$

where $f(N)$ may be a power series.

We define the efficiency of an asymptotic population as $\frac{K}{N}$, that is, as the number of organisms which can be maintained by a unit of environment.

We define the instability of the population as $\frac{dN}{dK}$, that is, as the rate of change of population size with size of the environment.

Comparing the situations represented by (5) and (6) we find that for all sufficiently high values of N, taking equal values of K, both efficiency and instability are higher in the non-social case, regardless of the absolute values of a and b, which must however be positive.

If negative values of the coefficients in (5) and (6) were permitted, the population would increase with negative environmental size, which is absurd.

The relation between number of individuals in the population at its upper asymptote and the of the environment (K) is shown in Figure 1 for social and non-social situations.

If the proportionality constants a and b are considered equal then the efficiency and instability of a social population are always lower than those of a non-social population.

Taking (7) as a power series, (5) and (6) can be considered as representing those spcial cases in which the first and second coefficients respectively are the only non-zero coefficients in

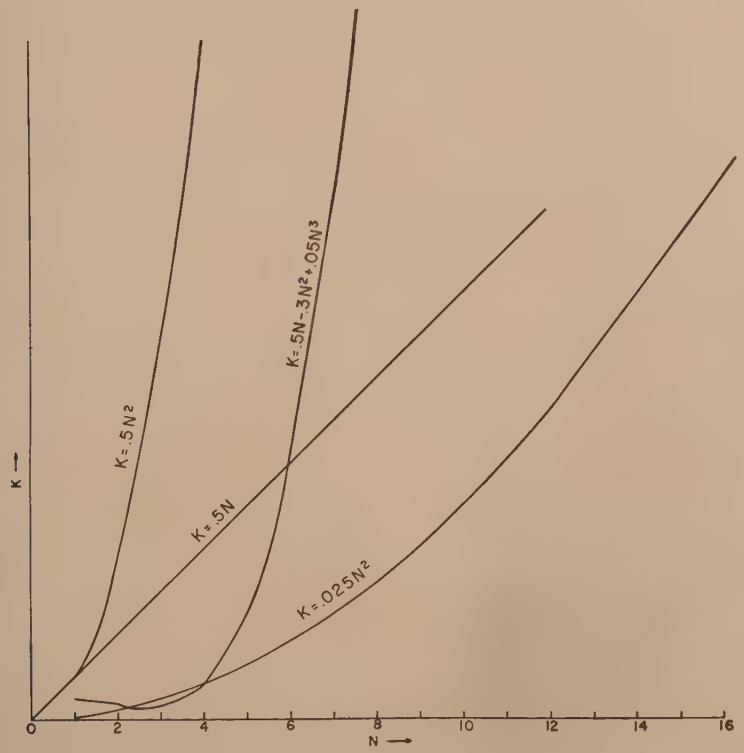

Fig. 1.

the series. Consider two closely related populations, one of which has a genetic tendency to follow (5) and the other (6). There is no *a priori* reason to consider the coefficients a and b equal. If, however, a is equal to b, the social population will show a lower efficiency and lower instability than the non-social population for all values of N. If $b < a$ then there will be an apparent "optimal density" effect when the two populations are compared. For sufficiently low values of N the social population will show a higher efficiency than the non-social population, but since the efficiency of the social population will decrease monotonically with K and N this does not constitute a true "optimal density" effect.

It seems advisable to limit the term "optimal density" to those situations in which the efficiency of a single population over some range of values of N is higher than that at either a lower or higher density value.

Optimal density can be discussed in this formulation in terms of the first three members of a power series:

$$aN, \quad bN^2, \quad cN^3 \cdots \tag{8}$$

The biological significance of the first three members of the series seems fairly clear. The expression aN refers to competition between individuals of the population for some material in the environment, disregarding all direct interactions between individuals. The term bN^2 refers to direct interaction between the individuals of the population, dependent on population density and independent of the environment, except in so far as this interaction affects the competition for environmental material between organisms. This is indicated in Figure 2b by uniting all the individuals of the population in a box, to indicate their interaction and drawing arrows to indicate the effect of this interaction on the competitive process.

The third-order term may represent the effect of groups of individuals on single individuals; for example, the effect of neighboring bands of monkeys on an individual monkey of one band or the effect of other family groups.

This is schematized as Figure 2c where the bracket groups the population into the system P which in turn affects each individual I_i.

The significance of higher members of the power series seems vague at present.

Taking a population which follows the form

$$K - aN - bN^2 - cN^3 = 0$$

a true optimal-density effect which does not violate previous considerations of possibility can result if, and only if,

a) b is negative
b) $b < a$

and

c) $b > c$

with a and c positive.

The relation between the coefficients is further restricted by the requirement that N and K must be positive and greater than zero. This restriction limits the relation between a, b, and c in a relatively stringent way. It has been found arithmetically that values of b which will produce an optimal-density effect without violating the conditions of K and N being positive will bear the relation shown in Figure 3 to a, with c taken as unity.

Optimal-density effects are impossible if $a < 2c$. For values of b above the values in the striped area of Figure 3 there exists a positive value of N for which K is negative. For values of b below this area efficiency decreases monotonically with N, so that no optimal-density effect is observed.

The maximal optimal-density effect is found in the range of $N = 2$ at $a = 3c$ to $N = 9$ at a

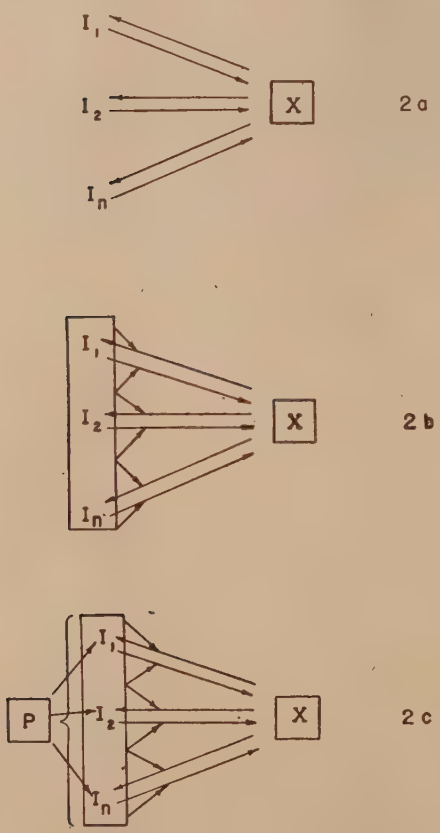

FIG. 2.

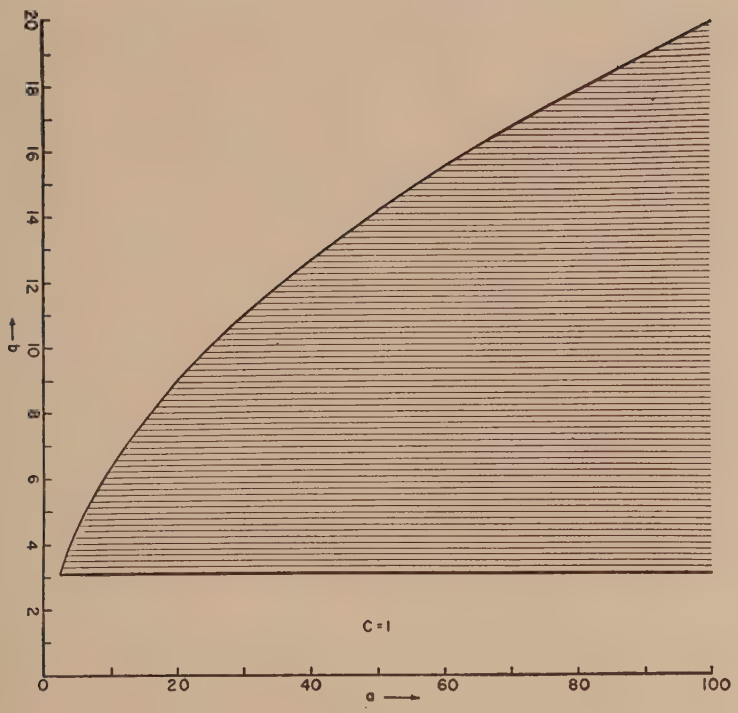

FIG. 3.

$= 1000c$. This is in surprisingly close agreement with the values reported for three experimental situations in which optimal density was measured.

In *Tribolium confusum* Maclagen (1932) and Chapman (1928) found that maximal reproduction per female occurred when two to four beetles were placed in each experimental container. Pratt (1943) found maximal longevity in *Daphnia magna* females at a density of five females in each 100 cc container of culture medium. Vetulani (1931) found maximal growth rates in mice raised two to four to a cage at 16° C. Other reported instances of optimal density effects do not seem so well substantiated as these three (see Allee *et al.* 1949). The significance of the agreement with the predicted optimal density level is not clear since so many simplifications have been introduced into the theory.

It should be made clear that the concept of population density has been used as an absolute number throughout this discussion. No restriction has been made on the geometric size of the environment except that it be sufficiently small to permit continual interaction between the organisms of the population. The consideration of population density as an absolute number is implicit in the common use of the term $\frac{K - aN}{K}$ in (1).

The form of Figures 1 and 3 is independent of the implicit assumptions of the Verhulst-Pearl equation. If the population consisted of a series of non-equivalent classes of animals (as in the formulations of Leslie 1948 and Slobodkin 1953), instead of the single class implicit in N, the same results would follow, if the number of animals in each category remained constant.

The system is probably completely inapplicable in any situation in which communication occurs between animals, as in bees. In such a situation the value of K is in a sense determined by the activity of the organisms.

Figure 1 is probably of significance as an indication of the environmental conditions which would permit social systems to evolve.

If the population exists in a highly variable environment there may be a selective advantage in developing higher-order interactions between organisms to provide stability at the cost of efficiency. Efficiency becomes of primary significance in relatively stable environments.

ACKNOWLEDGMENT

I am indebted to G. E. Hutchinson, Osborn Zoological Laboratory, Yale University, who has read and criticized the manuscript.

SUMMARY

Application of Hutchinson's (1947) notation for social interaction in an inter-species competition situation to the growth of single species populations permits the derivation of general conditions for the occurrence of optimal density effects in asymptotic populations.

If the relation between K (the "size" of the environment) and N (the number of animals at population equilibrium) is expressed as

$$K = aN + bN^2 + cN^3,$$

where a, b, c are constants, optimal density effects will be found whenever the ratio $a:b:c$ is such as to lie in the shaded portion of Figure 3.

In general, social populations have a lower efficiency and higher stability than non-social populations.

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THE BALANOID BIOME-TYPE OF INTERTIDAL ROCKY SHORES [1]

The concept of the biome and the biome-type has arisen entirely from studies of terrestrial ecology. Several other terms are partial or almost direct synonyms of these expressions; however, all point toward common ecological principles that, in my opinion, are best represented by the biome-type as recently defined and discussed by Allee, Emerson, Park, Park and Schmidt (1949).

Though biome-types are evident on land in relationships between climate, physiography and biotic development, attempts to demonstrate comparable ecological principles in other environments have not been convincing nor have they been widely accepted. Clements and Shelford (1939) suggested that certain specific marine communities be recognized as having the ecological status of a biome. Their Balanus-Littorina Biome suggested this type of ecological relationship in the intertidal zone. With qualifications in the light of later studies, particularly the work of Stephenson and Stephenson (1949) who recognize a balanoid midlittoral zone, the biome status of intertidal rocky shores can be further clarified. Though generally regarded as marine, intertidal areas are neither terrestrial nor oceanic; thus to regard a biotic development in these levels as a biome does not preclude other interpretations of submarine environments, such as proposed by Allee *et al.* (1949) to the effect that in the oceans we are dealing with a complex to be regarded as a single biome-type.

More specifically the Balanus-Littorina community of the North Pacific was singled out by Clements and Shelford for identification as a biome. They noted that their acquaintance with it is primarily in the Puget Sound area but pointed out that, though the biome is a band only a few feet high limited to the intertidal zone, ". . . it is apparently widely distributed around the North Pacific." These authors mentioned as dominant in this community three species of barnacles, *Balanus cariosus, B. glandula,* and *Chthamalus dalli,* and two species of mussels, *Mytilus edulis* and *M. californianus.* As the most characteristic motile forms they mentioned three littorine gastropods, *Littorina sitchana, L. scutulata* and

[1] Contribution No. 16, Oceanographic Institute, Florida State University.

Acmaea digitalis. The authors discussed the widely observed fact that, though climax in nature, communities of this sort may become established in a denuded area in a very few weeks. They included in the biome the development on sandy shores when beds of *Mytilus* form a substratum suitable for barnacles, snails, etc. Though indicative of some stability in sandy shorelines I believe such a biological development is too interrupted and too susceptible to shore changes to be regarded as having full biome status identical with that of the rocky shore.

Referring to a very similar climax community of the intertidal regions of the North Atlantic, Clements and Shelford (1939) stated that this biome, described by Newcombe (1935), is not the same since the characteristic component species are different. Instead of indicating this difference and stopping with that, I would utilize the biome-type concept presented by Allee *et al.* (1949) and thereby stress the ecological relations between rocky-shore intertidal climaxes generally. First it should be emphasized that the life forms as established in response to and contributing to the climatic and physiographic conditions of an area are of primary importance in interpreting biomes and, by contrast, taxonomic categories are not in themselves significant. Often, however, ecologists hesitate to carry this theoretical point to the extreme of recognizing identity in communities which are alike as to life forms yet different as to component species. The term "biome-type" surmounts this difficulty, recognizing ecological relationships without forcing questions of taxonomy. Thus the tropical rain forests of Africa and South America are of one biome-type and, returning to the illustrations under consideration, the rocky shore intertidal community of the east coast of the North Atlantic, for which Newcombe (1935) lists *Balanus balanoides, Littorina littorea* and *Fucus vesiculosus* as dominants, is of the same biome-type as its counterpart in the North Pacific. I base this primarily on the presence of the typical acorn or balanoid barnacle, *Balanus balanoides,* very similar in life form and ecological relations to the barnacles of the Pacific communities. *Fucus vesiculosus* is a co-dominant associated with the barnacle in this area without altering the environmental features to the extent of eliminating the abundant climax barnacle population. The *Littorina* of this community seems to compare ecologically with the related species of this genus on the Pacific Coast but, since such littorine snails are motile and are commonly more abundant above rather than centered in the mid-intertidal zone with the balanoids, I would consider such snails as common in but not characterizing the biome-type. This concurs with the proposed universal zonations of Stephenson and Stephenson (1949) who recognize a supralittoral fringe, characterized largely by representatives of the genus *Littorina,* existing above the midlittoral zone (intertidal in location) characterized by balanoid barnacles.

Thinking in terms of biome-types enables a still greater extension of these relationships. In the Florida Keys region I have studied the intertidal rocky shore community that seems to be the ecological counterpart of the *Balanus* community of Newcombe (1935) which I am also acquainted with along the northeastern coast. The low, pitted limestone shores of this area fronted by extensive shallows seldom present a bold exposure to the sea and often the mid-intertidal zone has a rather sparse barnacle fauna; however, the small acorn barnacle *Chthamalus stellatus* is widespread and abundant and crests and pinnacles are commonly well-populated by *Tetraclita squamosa,* a larger stalkless barnacle. On artifacts such as pilings and sea walls, which simulate natural rocky shores, *Balanus amphitrite* and *B. eburneus* are also found. This biotic development, though of scattered occurrence and quite different taxonomically, seems to belong to the same biome-type as the two previous examples.

One hesitates to extend such interpretations except from examples he has had an opportunity to analyze firsthand from this point-of-view; however, from more casual observations and from the literature, particularly the works of Stephenson and Stephenson whose summary (1949) suggested that an intertidal balanoid zone is quite universal on rocky shores, it seems likely that this biome-type is of world-wide occurrence. In view of the variations in tidal patterns and in wave action there are variations in this biome-type so great that detailed study will often be needed if the basic continuing pattern is to be sensed.

Since climate is such a basic factor in determining a biome, these illustrations of a biome-type over an extremely wide range of latitude call for special comment. Obviously many components of the climate vary considerably over this range; however, the alternate wetting and drying of intertidal areas is in itself a climatic feature ecologically far more significant than other aspects of the climate such as temperature that vary with respect to latitude, etc.

The question of the permanence of the rocky shore calls for consideration since to recognize a biome one must be certain that he has identified its true climax formation on stable physiographic features. Some ecologists emphasize the theoretical significance of physiographic stability even to the extent of considering large lakes, such as the Great Lakes, as transitory and thus as representing an early stage toward

a terrestrial climax development. Some rocky shores under consideration are every bit as transitory, eroding and even disappearing, giving way to sand. There are, however, many very stable rockbound coasts such as those formed by the exposure of continental bedrock.

For identification it is suggested that the ecological group discussed herein be referred to as the balanoid biome-type. The most characteristic dominant life form is the stalkless, crater-shaped balanoid barnacle. There is considerable variety as to the life forms that may occur as climax associates, and some of these will alter the environment but not to the extent of eliminating the characteristic barnacle fauna. To accept this involves numerous qualifications of the earlier suggestion of Clements and Shelford (1939) relating to the Balanus-Littorina community of the Pacific and essentially proposes the recognition of the balanoid or midlittoral zone of Stephenson and Stephenson (1949) as a biome-type. Though the interaction of biotic development with climate and physiographic features is to be considered as the same type of interaction found in biomes generally, this is one of those unspectacular biome-types in which the entire development amounts to little more than a simple immediate response to physical conditions. Certainly the ecologist would not look at intertidal rocky-shore communities and envision the biome concept; however, with that concept in mind such communities can be considered as a biome-type in comprehending the extension of ecological principles to diverse situations.

SUMMARY

Climax formations characteristic of intertidal rocky shore environments are discussed. Irrespective of geographic location the most characteristic dominant life form of such habitats is the stalkless, crater-shaped balanoid barnacle. Climax associates vary but do not alter the environment to the extent of eliminating these characteristic barnacles.

This biotic development with little or no succession leading to a climax of balanoids and associates is recognized as the Balanoid Biome-Type. The chief climatic feature governing this biome-type is the alternate wetting and drying of intertidal levels. Just as this feature is to be found on shores the world over, the Balanoid Biome-Type appears to have a world-wide distribution.

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THE "SPRING LIZARD" INDUSTRY: A FACTOR IN SALAMANDER DISTRIBUTION AND GENETICS

Salamanders are widely used in various sections of the Appalachians as a live bait for fish. In recent years the popularity of salamanders as fish bait has greatly increased until now thousands of them are collected for that purpose, especially in the mountainous parts of Georgia, North Carolina, South Carolina, Tennessee, Virginia, and undoubtedly in other states. Many of these salamanders are shipped to the nearby Piedmont and even to the Coastal Plain sections where in the last five to ten years there has been a great increase in the construction of farm ponds. In these ponds difficulties in management have been encountered due to the inadvertent introduction of objectionable species of fishes which have been used as bait. As a result, the sale of "spring lizards" has become a thriving business, bringing about the transportation of numerous salamanders into new and usually unfavorable regions. In Georgia, this has been especially true for the black-bellied salamander, *Desmognathus quadramaculatus*.

D. quadramaculatus is normally an inhabitant of mountain streams and is generally found at elevations above 2500 ft. Its range, according to S. C. Bishop's "Handbook of Salamanders" (Ithaca: Comstock, 1943), occupies the higher parts of the Appalachian Mountains from West Virginia southward to northern Georgia. In Georgia, I have taken several specimens in Rabun, Union, Fannin, Lumpkin, White, and

Habersham Counties—all in the northeastern part of the state. In June, 1951, D. W. Johnston collected two specimens (University of Georgia Collection Number 2) in the northern part of Banks County near its boundary with Habersham County. This site is at an elevation of about 2000 ft. and is located about 40 miles north of Athens, Georgia. At present this is the southernmost record of the natural occurrence of this animal in Georgia. However, in October, 1951, three specimens (U. of Ga. Col. No. 113) were taken by Charles Durant at Thompson's Lake, about 6 miles east of Athens. It should be emphatically pointed out that the Thompson's Lake area, having an elevation of about 700 ft., is definitely in Piedmont terrain and does not even superficially resemble the natural habitat of *D. quadramaculatus*—cold and rocky mountain streams flowing through wooded regions. The above-mentioned record does not represent a *bona fide* extension of the southern range of the black-bellied salamander but emphasizes the role of the "spring lizard" industry in the distribution of salamanders.

Indeed, it is possible that some transported animals will be released in areas favorable to their existence. Thus through man's activities salamanders may traverse important ecological barriers. In addition, this transportation of salamanders very likely will bring about the introduction of new genes and gene complexes into established populations, thereby possibly promoting the formation of populations which are genetically more homogeneous and which may create further difficulties for those persons attempting to clarify the subspecific relationships within the groups involved. Furthermore, this unnatural introduction of salamanders into new areas will undoubtedly give rise to apparently new extensions of ranges, especially for the species most commonly utilized by fishermen—*D. quadramaculatus, D. monticola, D. fuscus,* and *Pseudotriton ruber.*

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REVIEWS

TWO REVIEWS OF DICE'S "NATURAL COMMUNITIES"[1]

Principles of Community Ecology

Dr. Lee R. Dice, Director of the Institute of Human Biology and Professor of Zoology at the University of Michigan, has produced an important new textbook in the field of general ecology. His book is unlike any other thus far published and therefore presents a fresh approach to the teaching of this science. It is based entirely upon the exposition of concepts and principles of ecology. There is no description of specific communities and their habitats as the title might suggest, and there is no elaboration of environmental factors which forms such a large part of so many other texts. Stress is given to fundamental relationships between organisms of all kinds living in natural communities and between them and their environment. Plants and animals are considered in good balance as components of a unified community.

The treatment for the most part is very elementary. Hence the book is suitable for undergraduate students. This is one of the few textbooks of ecology which is easily within the grasp of beginning students and it is here that the need of a textbook has been felt so long. Dr. Dice has written his book in simple, straight-forward language. There is no complex terminology; technical terms are reduced to a minimum and are defined as used in the book; there is no complex mathematics; and controversial matters which might be confusing to the beginning student are discussed only in a few places. The discussion on each topic is brief; the coverage is extensive rather than intensive. No topic is penetrated deeply. Perhaps some of the obvious relationships or topics which are mentioned only casually might better have been omitted to allot more space for a more detailed discussion of some others. At times the reader is simply told that a certain factor has an important influence on the community but the nature of its importance is neither revealed nor illustrated. On the other hand, frequent examples of a concrete nature are included to illustrate the exposition yet none is carried into unnecessary detail. Pertinent facts and conclusions only are given, but references to more detailed studies are often cited. At times the discussion is perhaps oversimplified and the relationships described should be self-evident to any student who reaches the level of a college course in ecology. Such might be of interest, however, to the general reader who has not had much experience in field biology.

There are 23 chapters on the nature of communities and community ecology; methods of studying communities and populations, their variations, fluctuations, and equilibrium; reciprocal relations of environmental factors and communities; food relations and animal behavior; succession, classification, evolution, and philosophy of communities. It seems that more chapters were created than are really necessary. One advantage of having many short chapters, however, is the convenience of making unit reading assignments to students and another is the ease of arranging the sequence to fit the needs of the instructor. The sequence as presented in the book does not always appear logical. For example, chapters on physical factors that affect communities are widely separated from the chapter on reciprocal effects of communities on physical factors; a chapter on fluctuation of populations is removed from the chapter on estimation of populations; and discussion of food relations is far removed from the treatment of ecological relations between species. The reviewer realizes, of course, that it is impossible to arrange closely interrelated subjects in a linear sequence which will show natural relationship equally well throughout.

The author of this text looks at communities from every significant angle. A brief outline is given of various aspects of community dynamics—relations of physical factors to both individuals and groups, life history of species, population fluctuations, interaction of species, group behavior, aspection, annuation and cycles, invasion, succession, and evolution. The conventional pattern of describing community organization was not adopted. The discussion is confined to the basic principles involved which are true of all natural communities. No specific one is treated in detail although examples are given from all kinds of terrestrial and aquatic communities. At times the reading becomes somewhat monotonous, and the text resembles an annotated catalogue of ecological relationships. It is interesting to note that while the discussion is confined to community relations, reference is made more often to a text in autecology than to any other. At least this may emphasize the intrinsic relationship between autecology and synecology.

[1] **Dice, L. R.** 1952. Natural communities. x + 547 pp., 52 figs. Ann Arbor: University of Michigan Press. $5.50.

Dr. Dice is critical in his approach to methods used in ecological study and in the interpretation of published results. He is realistic about the value of some studies and points out the limitation of methods of research which have developed as well as the knowledge thus far gained. Frequently he points out to the reader the need for more and better information on certain topics which should be suggestive to the serious student.

Some terms (e.g. population, association, society, family, symbiosis, etc.) are given precise definition as used in the text. Needless to say they are not universally used as they are in this text. Two new terms are proposed: "microstand" which occupies what some authors call a micro-habitat; and "two-parent family" which consists of both parents with their offspring. The term "symbiosis" is used in the sense of "coactions" of some authors rather than in the restricted sense of mutual benefit as employed by many biologists. McDougall's designations of conjunctive and disjunctive symbiosis, which have never been widely accepted, are adopted. Thus "symbiosis" in its restricted meaning here becomes "mutually beneficial conjunctive symbiosis."

Many references to ecological literature are cited, but it seems to this reviewer that too often reference was made to secondary sources rather than to primary sources. Also, no distinction is made between a reference to another text for further reading on the subject and a reference to the authority for the statement made. To the uninitiated many citations will probably be incorrectly regarded as the source of information.

Only one typographical error was noted by this reviewer and few errors of fact. Eelgrass, a spermatophyte, is called a seaweed, which term generally refers to algae. Also, eelgrass is given as an example of an organism which fluctuates without a definite cycle. Actually it is only since the recent extremely severe epidemic of eelgrass disease that eelgrass has failed to recover from the wasting disease in a cyclical pattern. Previously, periods of eelgrass decline were correlated with periods of extreme north declination of the moon as shown by Neil Stevens.

Dr. Dice is very critical in his discussion of succession, both of concepts and of published studies. As much or more attention is focused on exceptions and irregularities as on the usual processes. Without doubt the concept has been over-worked and over-simplified by some ecologists and insufficient attention has been given to the variety of possibilities in succession by some writers in the past. However, Dr. Dice seems to lean over backwards to correct the situation in a hurry. His statement that the "ideal climax" is "seldom or never realized" will be difficult to defend. The fundamental processes in this one case are somewhat neglected in the book in the interest of variations of the basic theme. This point of view will doubtless be well received in some quarters where the concept of succession has recently been attacked. Some have gone so far as to question the existence of such a process.

In reference to the subject of community nomenclature the statement that "Complete agreement on this subject is still lacking" is a gross understatement. Controversial matters are largely confined to the last few chapters, but they are aired thoroughly in this chapter. The book naturally follows the system of Biotic Provinces devised earlier by Dr. Dice. It is also natural that it would be defended and not severely criticized. He accuses "biome ecologists" of ignoring successional changes. It seems to the reviewer that such is only true in the mapping of the climatic climax areas and not in the field studies themselves. Dr. Dice also criticizes them because the biomes do not have geographic unity, apparently without realizing that biomes and their subdivisions are based on biotic relations rather than geographic relations. At the same time he sometimes regards his biotic provinces as single communities when in certain cases they are geographic groups of diverse communities. In the same vein he is critical of the published boundary lines of biomes but is quite satisfied with those of biotic provinces. These matters depend, of course, on which side of the fence one stands. Stress is given to the claim that biotic provinces are centers of taxonomic differentiation, but it is not shown that this is any more true in his system than in the biome system. However, a note of optimism and of the prospect of harmony is sounded at the end of the discussion on community classification by saying, "Biomes and biotic provinces are not necessarily to be considered as mutually exclusive and competing systems of ecologic classification, but rather as more or less supplementary to each other." This is a most encouraging attitude.

Originally the book was intended to include a chapter or two on human communities but space limitations did not permit. Dr. Dice has promised another book on that subject to which we shall look forward with anticipated pleasure.

There are only 52 illustrations in 486 pages of text. Most of them serve a useful purpose, but considering the limitations of the number of figures a few did not seem to be too well selected. Most of them are redrawn from other sources. A few could have been described just as effectively as being shown in visual form.

There are about 1,000 references to ecological literature in the bibliography. Some of these are repeated at the end of each chapter as suggestions for further reading on the topic discussed. There is a good index. The book is reasonably priced considering the cost of books today.

While this reviewer has tended to single out points on which disagreement might arise or items in which improvement might be made, they are decidedly in the minority. All in all, the purpose for which this book was written has certainly been met by an excellent performance. It gives promise of being a very useful, teachable, and successful text for the instruction of undergraduate and beginning students in general ecology and for reading by the informed public. Many laymen as well as students are now turning their attention to ecology and its importance to the welfare of man. Here they will find an easily understandable and digestible introduction to the principles of community ecology.

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Methodology and the Community Concept

The title of this comprehensive book may prove misleading to some biologists. For example, a Chicago Area confrere was searching for modern literature that could be used in his seminar to contribute faunal data that would sustain or discredit the position that the southeastern flora of the United States (the southeastern evergreen forest of Lucy Braun) was a legitimate part of the deciduous forest biome of eastern North America, or whether it should form a separate biome. His copy of Dice's "Natural Communities" not having arrived, he wished to borrow my, as yet unread, review copy. He returned the book later in quite a pique, and I fear regrettably prejudiced for, of course, there was no discussion of any natural community in the systematic geographic and biotic sense that he felt the title warranted.

On the other hand the first sentence of the Preface states: "The purpose of this book is to describe the more important methods and concepts . . . dealing with natural communities." It is this purpose, rather than the title of the book, that is our chief concern.

On the whole the book justifies this stated purpose. If one wished to have a student look into the matter of how natural populations of vertebrates in grassland or forest could be studied, this book would serve as an admirable point of orientation. It is written in a very readable style, one which tends to lessen "reader resistance," on the whole well illustrated, and by one of the deans of American mammalogy.

The first chapter is concerned with terms and general methods in community study. The community concept is emphasized.

The second chapter is descriptive and has to do chiefly with various levels of community organization, including biotic province and regional community, association, stand, stratum, microstand, microassociation, community type, habitat, and ecosystem. The microstand is a new term proposed (p. 19) for a minor community that is not of sufficient extent or importance to be called a stand. As one of several examples given for the microstand is the decaying log. One is not certain that this term is necessary, since the decaying log is also well known as a habitat, and is a rather well documented microsere, from its pristine condition to its eventual mounding into the community floor in the process of organic soil formation. Other examples of microstands given are dung, decomposing carcasses, nests of social insects, and clumps of herbs or shrubs together with their associated organisms.

The ecosystem is used in the sense of Tansley and of Lindeman, as the biotic community plus the physical habitat (Fig. 4). It should be remembered that others regard the community as composed of both the biotic and physical substrates in an almost indecipherable compound at both the operational and philosophical level, *viz.*, the ecosystem and the community are the same.

The third and fourth chapters deal with methods for the description and mensuration of communities and estimation of populations. These are concise and most useful. Chapter four opens with some pertinent remarks anent taxonomy and ecology, remarks that every one should read, and have his students read. Despite this, the goal is hardly feasible, and as invertebrate taxonomy gathers momentum this goal will recede rather than approach. Professor Dice states (p. 63): "The ecologist himself should be fully competent to identify the group of organisms which is receiving most of his attention in the field." He is talking here of identifications at the species level. I agree with this and the rest of the author's remarks here, or rather, I should like to feel that I share his jest. In most institutions of higher learning in the United States taxonomy is

given short attention, and not too much attention to field work either. In the reviewer's experience it takes about half of an academic career to get on familiar speaking terms with a family of beetles.

The fifth chapter (physical factors of habitats that affect communities), sixth (effects on communities of fluctuations in the physical conditions of their habitats), and seventh (food relations within communities) bring together the data on physical influences and trophic relations. Then come two chapters on fluctuations: chapter eight (those within populations) and nine (those in the composition of communities). The relations of organisms to their ecosystems (chapter 10), home ranges and territories (11), effects of social behavior on the community (12), ecologic relations between species (13), community equilibration (14), effects of communities on physical habitats (15), ecologic succession (16), local and geographic variation within communities (17), inter-community relations (18), classification of various types of associations (19), and the larger units of community classification, *viz.*, community type, life zone, biome, and biotic province, including a comparative criticism (20), serve to document further the analysis of methods and concepts that bear upon community ecology.

In chapter twelve, having to do with social behavior, the term "society" is regarded with disfavor since it has been used with different connotations by botanists and zoologists. The author feels that "social group" should be used rather than "society" in any case where confusion might arise, and selects "band" to mean "a concrete social group of mobile animals of any kind, composed of 2 or more individuals" (p. 266).

Chapter nineteen, of interest to those who tend to worry over ecological taxonomy, should provoke discussion. The author states frankly that since ecologists have been unable to agree on any classification of communities according to rank, the system that he sets forth will not be acceptable to all. He separates communities into "concrete" and "abstract" communities. The former are thought of as assemblages in which the component organisms are either directly or indirectly associated with one another; the latter are communities that are based on abstractions, and composed of those concrete communities that are sufficiently similar to be classed together. The "association" is an abstract community composed of an assemblage of stands. As used in this book, the association is an abstract concept, and the stand is the concrete unit of community classification. The "stand" is regarded as the most important unit of ecologic classification. It is an actual community that exists at a given time and covers a particular area; included is the view that this is a community of importance and the area covered is substantial. Since the term association has been thought of as the end product of a sere, or climax community, by many ecologists connfusion results, but, it must be added, a confusion that was to be inferred in the author's preliminary paragraph in this chapter.

The reviewer found the last three chapters specially interesting. They are chapter 21 (communities of the past), 22 (evolution of communities), and 23 (philosophy of communities).

Since great changes in communities have occurred in the course of geologic time, the author brings together the methods for the study of such units. These include succession, pollen analysis, organic remains, and evidence from fossil beds.

Communities must have arisen through a long course of evolution. In the twenty-second chapter the author discusses the evolution of various ranks of communities; the ways in which a community may change (by addition of species, loss of species, evolutionary change of resident species); special features of community evolution, including adaptive radiation, the rôle of natural selection, areal effects, isolation, and changes in climate and physiography. The chapter terminates with a discussion of evolutionary rates of communities, their ultimate limits and their adaptations.

The last chapter (23) discusses the community as a unit, and then examines the community concept from the individualistic versus the organismic viewpoint, ending with the place of the community in emergent evolution.

Each chapter has a short list of selected references. In addition, there is a terminal bibliography of some forty-eight pages. The ten page index is comprehensive but not as complete as some would wish.

Two minor matters may be noted. The reviewer was surprised to find that J. R. Carpenter's 1938 "Ecological Glossary" was not included in the index or bibliography of a comprehensive book in which a good deal of community terminology is discussed.

In the fourth chapter, dealing with methods of estimating populations, the reviewer feels that there is insufficient attention given to substrate invertebrate populations. With growing emphasis on soil populations, microhabitats, and their microclimates, research methods reflect this increased activity. On page 74 the flotation method and the Berlese-Silvestri-Tullberg funnel methods are briefly noted, and supported by three references. A critical evaluation of these and other methods, their advantages and

drawbacks, even a good illustration, or some circumstantial data would assist the reader and give a more even distribution of emphasis as between vertebrate and invertebrate animals.

Finally, Dr. Dice's volume fills a needed gap in the literature and justifies the purpose of the book as stated in his preface and in this review.

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ECOLOGY OF SESSILE MARINE ORGANISMS[1]

Marine fouling results from the growth of organisms on structures submerged in the sea; its practical importance is briefly but clearly summarized in Part I. On ships it results in increased resistance to movement through the water, efficiency is reduced, maximum speed falls and an increase in fuel consumption and wear and tear on the engines result. Removal of fouling entails costly docking (over 100 million dollars in the U. S. in 1938) and serious loss of ships' time. In time of war, when high efficiency and speed are of great importance and when time in dock reduces the strength of a navy, the fouling problem becomes increasingly acute. The growth of these organisms on buoys, mines and antisubmarine nets, by increasing the weight and resistance to water currents, can cause them to float at incorrect depths or even sink them; while such attachments on sonic devices greatly reduce both range and efficiency.

Part III deals with the theory and practice of fouling prevention. Before the advent of iron ships, all preparations aimed both at fouling prevention and at protection from marine borers; in fact, before the advent of copper sheathing most protective methods (for instance lead sheathing) appear to have been efficient only against attack by borers. It was not till the latter part of the eighteenth century that the general use of copper sheathing provided efficient antifouling. Almost immediately a serious problem arose—in seawater copper causes serious corrosion of iron structures. The British Navy called on the assistance of Sir Humphry Davy and received his clear explanations. As iron and, later, steel ships replaced wooden ones, this corrosive effect of copper became of increasing importance and attention was directed to antifouling paints.

From a careful review of earlier work and extensive research carried out for this project, the action of antifouling paints has become clear. A satisfactory protective paint must maintain a certain minimum level of soluble toxic substances. Modern antifouling paints can be divided into two classes. In the first class are those in which a very heavy load of toxic substance is held in an insoluble matrix while in the second class a much lighter toxic load is bound by a soluble matrix. In the former, solution of the toxic progresses by continuous contact of the toxic particles, so penetrating to deeper and deeper levels beneath the surface of the insoluble matrix. In the latter type the whole paint, both toxic and matrix, slowly dissolves. It will be readily seen that the toxic load needed for effective paints will vary greatly with the type considered. Yet in 1928 the American Society for Testing Materials issued specifications for antifouling paints that ignore the difference in types and are therefore quite valueless. Design of antifouling paints has now moved from the cookery class to the scientific laboratory.

To ecologists the middle third of the book on the "Biology of Fouling" will prove of greatest interest. Not only has the previous work been carefully considered but a mass of excellent research carried out directly for this project is summarized. As much of this work has not been widely reported, here is the only place where it is readily available. The best way to give an idea of the breadth of the field covered is to list the chapter headings—"The Fouling Community," "Temporal Sequences and Biotic Successions," "The Seasonal Sequence," "Quantitative Aspects of Fouling," "Geographical Distribution," "Relations to Local Environments," "The Principal Fouling Organisms," "Species Recorded from Fouling." Many of these chapters read like good papers in our best ecological journals. No marine biologist can afford to ignore this section which is a model summary of the ecology of the attachment of marine organisms. It should be required reading for every senior student in marine biology.

This work is a readable handbook in the technology of marine fouling and, at the same time, a remarkable contribution to marine biology. Because of its broad basis in pure research, not only has it answered many vital problems of practical importance but has opened the way to further advances both in pure science and in practical technology. Over a hundred

[1] **Woods Hole Oceanographic Institution.** 1952. Marine fouling and its prevention (prepared for Bureau of Ships, Navy Department). Annapolis, Maryland: United States Naval Institute. 388 pp., $10.00.

years ago the British Navy wisely threw their problems in the lap of Sir Humphry Davy and received answers from pure science on which we have built ever since. In 1940 the Bureau of Ships, U. S. Navy Department handed their problem to the Woods Hole Oceanographic Institution. Again the answers from science have been clear and of abiding value. Many of us have viewed with misgiving the inevitable entry of government into the research field. But this work shows how, when a government department, guided by an enlightened policy joins with a scientific institution under wise leadership, the results can be beneficial both to science and to technology.

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Bertalanffian Organismicism [1]

The literature by von Bertalanffy and his followers, widely scattered in foreign journals, is at last organized for English speaking readers! An evaluation of this book for members of the Ecological Society of America puts me at crossed purposes. On the one hand, for a professional group which in the main is laboring under the handicap of an outmoded scientific philosophy strongly rooted in the mechanistic causality of 19th century physics, I should not discourage any reading in this field whatever. On the other hand, there is information here of much value to ecologists, but this book may not choose the easiest way. Unless one is already somewhat familiar with the terrain, I hesitate to suggest riding your uprooted log down the rapids of von Bertalanffy's highly personalized route.

For understanding a book, one goes first to the title. This one is not inappropriate, after one knows the book. Yet its inadequacy by no means approaches that already classical case of the dollar-angling editor who dubbed Conard's translation of "Das Pflanzenleben der Donauländer" as "The background of plant ecology." The present book, not concerned with marriage counseling or personal health, is not a survey of philosophers' thoughts. It is a tight concentrated detailed portrayal of von Bertalanffian Organismicism. (Organicism is a different word.) Perhaps the name of the author alone makes any title unnecessary. Since important developments have arisen through this school, it should be read either by those who may wish to become devout converts and one-prophet followers, or by those who would like to place the school among contemporary lines of thought.

We find that the book is based on a "German original," "Das biologische Weltbild. Die Stellung des Lebens in Natur und Wissenschaft," published in Switzerland in 1949. The translator, if this present volume is a translation, is not named. He deserves credit, for in the always difficult task of putting philosophical German into readable English, he has succeeded remarkably well. There are relatively few instances where I felt vaguely that had I the original German I would use other English equivalents. Comments are frequent concerning a future larger and technical volume, replete with mathematical considerations. At times, this intent has led to such abbreviation of the present phrasing as to make it appear only a preview. There are numerous references and quotations in the book, almost all to von Bertalanffy himself, and his followers. The references are listed at the end (in seven sections, requiring up to seven "tries" to locate a paper), and here one sees how outstandingly German the movement has been. In this respect, the present book is a distinct service to the English-speaking public, aided by the fact that its author has moved from the University of Vienna to the University of Ottawa. The seven sections of the references will greatly help those who wish to delve deeper: 1. "Publications Pertinent to the Foundation of the Organismic Conception," all by von Bertalanffy; 2. "Discussions of the Organismic Conception"; 3. "Application to Individual Problems"; 4. "Further Developments"; 5. "Similar Viewpoints from Other Sources"; 6. "Recent work Pertinent to Organismic Biology": and 7. "Suggested Readings on Modern Biological Thought." This last is the shortest list, all in English, knowledge of which would allow the reader to make "an evaluation of modern biologic thought" in a sense totally opposed to that of the title of this book.

There are six chapters in the book, each with numbered subheadings. These guide us from a discussion of older philosophic alternatives, through basic ideas, the Organismic Conception itself, its application in various fields, and then to epistemological consequences. This last ends in a burst of unabashed pride in this brainchild, when it is raised aloft as the keystone in

[1] **Bertalanffy, Ludwig von.** 1952. Problems of life. An evaluation of modern biological thought. xi + 216 pages. New York: J. Wiley. London: Watts. $4.00.

a new conception of the world, the General System Theory.

In the first chapter, "Basic Conceptions on the Problem of Life," mechanism and vitalism are discussed as two fundamental and antithetical biological concepts with their beginnings in Greek philosophy, both of which are at present inadequate. Within mechanism, most biological research and thought have been determined by three leading ideas: the analytic and summative; the machine-theoretical, and the reaction-theoretical concepts. The first involves analysis into parts and summation together. The second involves a certain structural organization which by its nature functions as a machine in set and definite ways. The third involves a stimulus-response scheme whereby the machine is a more or less passive body, subject to action only through outside influences. All these attitudes can be easily recognized in our ecological research. Transcending all these and opposed to all, the Organismic Conception considers the system as a whole (not to be broken down, or added together); it is dynamic (without emphasis on the static form); it itself is a primary activity (rather than activated from outside). The author acknowledges that "similar conceptions have been found necessary, and have been evolved, in the most diverse fields of biology, as well as in the neighboring sciences. . . ." He recommends retaining the term "Organismic Conception" for "an attitude which has already become very general and largely anonymous," since "the author was probably the first [1926] to develop the new standpoint in a scientifically and logically consistent form." On that last, I will let other authors speak for themselves.

The second chapter "Levels of Organization" takes us successively from discussions of electrons, protons, atoms and molecules, through viruses and cells, to organisms as commonly recognized. The structure of organisms reveals a hierarchical pattern. Based on Woodger, seven different types of hierarchies are described, all capable of coexisting in the organism. After defining the individual, he discusses the world of "supra-individual organizations" or biocoenoses. We are reminded here and elsewhere that the Organismic Conception has been applied by a German forester in describing a *Dauerwald,* apparently the sole convert to the idea, for application to a supra-individual system. These five pages are the part which logically has most value to students of plant and animal communities. We find however no recognition or evaluation of the voluminous biologists' literature on the subject, both in Europe and America. Nor does the author himself consider the problem of the degrees of integration of the system at any one level, a problem so important in these "supra-individual organizations" of plant and animal communities.

In chapter three, "The Unitary Conception of the Processes of Life," the author applies his basic ideas to various phenomena on the individual level. Embryology, one of his first and major interests, receives considerable attention, with the embryo developing, taking from the environment, giving to the environment, but still maintaining itself as an integrated distinct organization. In the discussion of genetics, we find the author emphasizing the necessity of an Organismic Conception of heredity, especially in regard to a consideration of the genome in its entirety, rather than separated studies of each particulate gene. With less application of organismicism, selection, speciation, and the multiplicity of non-adaptive variations are separately treated. Then recognizing that most of the discussion has dwelt on form and structure ("organization") and functions and processes ("dynamic flow of processes"), in the sixth section he considers the time factor under the designation of "The Historical Character of Life," bringing in his theme by referring to the organism as a spatio-temporal whole. In a concluding application, "the field of the processes in the central nervous system and of behavior . . . belong to those whose recent developments demonstrate impressively the rise of organismic conceptions."

In chapter four, "Laws of Life," the three sections are distinct. In 1. "The Stream of Life," we finally reach definitions and discussions of the "open system" and the "steady state," two terms which are coming into popular usage, and should not be more mystifying than necessary. ". . . The characteristic state in which we find the living organism can be defined by stating that it is not a closed system with respect to its surroundings but an *open system* which continually gives up matter to the outer world and takes in matter from it, but which maintains itself in this continuous exchange in a *steady state,* or approaches such steady state in its variations in time." At the head of the chapter is a quotation from Goethe's "Duration in Change" expressing the same idea in romantic poetry; and the first words below identify the concept with that of Heraclitus of Ephesus, who in antiquity is quoted as having said; "You cannot step into the same river twice; for fresh water is for ever flowing towards you." At the risk of juxtaposing the cultured and the uncultured, I am tempted to go back further, with the thought that any contemplative cannibal, considering his in-come and his out-go while he himself remained the same, might have made a similar observation, though inelegantly, and certainly without referring to himself as an open system in a steady state. As applied to the modern science of physics, von Bertalanffy writes, "According to

definition, the second law of thermodynamics applies only to closed systems; it does not define the steady state." Following the studies of others on the thermodynamics of irreversible processes, "the author considers it as one of his most important achievements to have given from the biological side an impetus to this development in physics." For the common run of us, the open system is probably to be looked upon as a refinement of the "dynamic equilibrium" of more familiar thought. 2. "The Definition of the Organism" leads us to "A living organism is a hierarchical order of open systems which maintains itself in the exchange of components by virtue of its system conditions," to which he is urged to add that they also have a historical character. For those who use the ideas of "subject matter" and "point of view" for coordinating schools of thought, this statement is quickly seen as the definition of one subject matter in terms of four of the possible points of view. In 3. "The System Conception of the Organism—a Basis for Exact Biology," the author looks forward. A large number of detailed biological fields of investigation are surveyed, for which "In the following volume a more systematic presentation in mathematical language will be given." "From the position now reached new insight can be obtained into many problems, leading to some extent to exact quantitative laws for basic phenomena of life." ". . . The new theory opens up the way to basic problems of the living world, in which the deepest secret of life was thought to be included." "So we shall hardly be mistaken in assuming that with these principles we are near the very roots of the fundamental biological problems."

Under the title "Life and Knowledge," chapter five, there are various philosophical considerations in biology and physics, revolving around the idea that their basic laws are fundamentally different and that those of biology are not eventually reduceable to those of physics. ("Biology" is zoology: botany plays a minor role in the book.) In acknowledged exception to this attitude, several fields of microphysical phenomena in biology are described, such as radiation genetics. In concluding this chapter, a new and important attitude is brought in. "All laws of nature are of a statistical nature. They are statements about the average behavior of collectives." This attitude is shown to be applicable at various levels of organization, for physical particles, individuals, and supra-individual units of life. The last is an idea which in the reviewer's opinion no one has yet developed. It is not to be confused with the totally different statistical analyses of sampling data, currently so popular. When the idea does affect our comprehension of the basic nature of vegetation and of biologic communities, it may well have important repercussions on those sampling procedures.

At this point, the reader may be aware of an extraneous development in his own mind. Here is a situation which we find time and time again in episodes in the historical development of science, art, religion and philosophy. One of the finest examples of the Organismic Conception is Bertalanffian Organismicism itself, a child of our human nature and our anthropoid ancestry, and only an attempted facsimile of external nature. Conceived in the psychologic attributes of a normal human personality which seeks to enlarge its own greatness, and amplified by that normal sociologic phenomenon whereby others tend to follow a leader and mold themselves in his image without further thought, this school has itself become an open system in a steady state, maintaining itself in form and function and time, strongly resisting hybridization, amalgamation, or such absorption as would destroy its purity and separate identity. It is even a manifestation of that phenomenon the author noticed in the evolution of species, whereby nature is not "a calculating merchant; rather she looks like a whimsical artist, creative out of an exuberant fantasy. . . . On the one hand, nature is a niggard when she insists on abolishing, say, an already minute rudimentary organ; this little economy having, as maintained by the theory of selection, enough advantage to be decisive in the struggle for existence. On the other hand, she produces a wealth of color, form, and other creations, which, as far as we can see, is completely useless. . . . This productivity and joy of creation seems to be expressed in the 'horizontal' multiplicity of forms on the same level of organization . . . which can, but need not necessarily, be considered as 'useful.'"

In the final chapter, "The Unity of Science," the author, with unusual modesty, admits that If we survey the various fields of modern science, we notice a dramatic and amazing evolution. Similar conceptions and principles have arisen in quite different realms, although this parallelism of ideas is the result of independent developments, and the workers in the individual fields are hardly aware of the common trend." He reviews the situation in physics and biology, goes on into psychology and philosophy. In this last, he finally speaks of Smuts, Lloyd Morgan, Whitehead, Meyer-Abich and others, all associated with very similar ideas. None of these however are actually referred to by bibliographic reference, and one strongly suspects that his knowledge is secondhand, by way of Woodger. William Morton Wheeler is referred to only by a single German paper, assumed by his daughter, Miss Adeline E. Wheeler, in correspondence to me, to be a

translation of an article that had appeared in the Scientific Monthly.

In concluding this chapter, we reach in a sense the pinnacle of the volume. "From the statements we have made, a stupendous perspective emerges, a vista towards a hitherto unsuspected unit of the conception of the world. Similar general principles have evolved everywhere. . . . What is the origin of these correspondences? We answer this question by the *claim for a new realm of science*, which we call General System Theory. It is a logico-mathematical field, the subject matter of which is the formulation and derivation of those principles which hold for systems in general." "General System Theory . . . will have a momentous share in future developments." ". . . General system theory may be considered as a step towards that *Mathesis universalis* which Leibniz dreamed of, a comprehensive semantic system including the various sciences. Perhaps it can be said that in the modern dynamic conception a theory of systems may play a role similar to that of Aristotelian logic in Antiquity." (I am a mere reviewer, and here I am hushed into awed silence.)

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Pioneer Effort in Mexican Biogeography [1]

Modern work on the distribution and taxonomy of Mexican birds and mammals dates from the turn-of-the-century explorations of that country by E. W. Nelson and E. A. Goldman under the auspices of the old Division of Economic Ornithology and Mammalogy, formerly a part of the U. S. Department of Agriculture. With Goldman acting as Nelson's assistant, at the ages of 18 and 36, respectively, they undertook a distributional survey of the higher vertebrates of Mexico as a part of the large-scale program of research on life-zones developed by C. H. Merriam in the 1890's. Almost continuous field work from 1892 to 1906 enabled them to visit all states of Mexico, most of its faunistically significant offshore islands, and southwestern Guatemala. Specimens obtained and now in the United States National Museum totalled 17,400 mammals and 12,400 birds, plus a considerable number of reptiles, amphibians, and plants.

In the years after 1906, other interests and duties prevented Nelson and Goldman from exploiting fully their enormous fund of data on Mexico. A series of short papers in the first decades of the century skimmed off most of the taxonomic novelties among the birds and mammals they collected; but because no comprehensive report of the collections ever appeared, there is no record of the full extent of their discoveries, and many facts known to them independently entered the usable literature only in subsequent years, from the reports of other collectors. Most, but definitely not all, of the birds collected were used in the preparation of the monumental "Birds of North and Middle America" by Ridgway and Friedmann. Otherwise, beside the report here reviewed, three papers of substance resulted: one on plant records from Lower California (by Goldman), another on tailless amphibians of Mexico (by Remington Kellogg), and the last, certainly the most comprehensive and scholarly of them all, on the geography and natural resources of Lower California (by Nelson). Nelson died in 1934, Goldman in 1946, and as H. H. T. Jackson remarks in his preface to this last report, "immeasureable information that was never preserved on paper vanished with the passing of these two really great naturalists." Some hint of this is provided by Goldman in a brief comparison of conditions at La Barca, Jalisco, in 1903 and in 1935–36 (pp. 172–174).

The bulk of the text (295 pp.) consists of an itinerary and an alphabetic catalog of localities visited by Nelson and Goldman. For each locality there are dates of visits together with notes on local conditions of climate, physiography, and vegetation and on chronology and distances of travel. Much interesting and valuable is available here to students of Mexican geography, even though its overall impact was lost when the original journal was fragmented into alphabetizable segments.

The remainder consists of an 18-page sketch of the geography of Mexico as a whole and a 128-page section on life-zones and biotic provinces of Mexico, with long lists of trees and shrubs, birds, and mammals present in each. Analysis by life-zones of Merriam as well as by biotic provinces (earlier described and mapped by Goldman and Moore, Jour. Mamm., 26:347–360, 1945) is only preliminary in scope and so declared by the author. Recent comprehensive studies of various groups of birds and mammals and of the faunas of various sections of Mexico have quickly made the lists in this book more or less out-of-date. In the lists of birds, the taxonomy is partly that of Ridgway and partly

[1] **Goldman, Edward Alphonso.** 1951. Biological investigations in Mexico. xiv + 476 pp., 76 plates, 1 folding map. Smithsonian Misc. Coll., vol. 115, $4.50.

that of Hellmayr, with the result that certain pairs of names representing synonyms of one race are treated in different sections and in the index as distinct taxonomic entities. I detected omission of one long-known Guerreran endemic described by Nelson. It would seem that if the birds and mammals had been listed in taxonomic order, with brief annotations on distribution (as are given anyway) and with columnar records of *known* occurrences in zones and provinces, the end-product would have enjoyed a longer period of usefulness than the elaborate breakdown by biotic units that was published. Also, such errors as mentioned above would have been detected more easily.

For the areas that members of the Merriam school studied, they attempted to work out distribution of birds and mammals and to accompany this by an analysis of life-zones. As pioneers in the biological exploration of Mexico, Nelson and Goldman could not, at least at first, have realized the staggering enormity of what they undertook. As a matter of fact, the definitive reports on birds and mammals, ambitiously planned in earlier years, never appeared. Today, only after decades of additional field work by many persons, and with collections of birds totalling easily ten times the number amassed by Nelson and Goldman, is it possible, through the cooperation of several experts, to draft a reasonably complete distributional check-list of the birds of Mexico. Because of complex physiography and the resulting abundance of ecological islands in Mexico, it is necessary to fragment the mosaic of biotas in some way for purposes of analysis. This can probably best be done by vegetation-type. At present, for example, some knowledge is needed of the internal structure of the fauna of subtropical cloud forest, within its metropolis and at its various outposts, as in Jalisco, Sinaloa, and San Luis Potosí. Comparable studies of other major vegetation-types will later lead to the over-all picture that Nelson and Goldman had hoped to provide.

Comments on the terminal parts of this work should not reflect on the record of travel and field observations. Goldman's book is an important historical document, useful to ecologists, geographers, and historians. Anyone seriously interested in Mexico should be acquainted with this volume, for its text and also for its collection of 136 excellent photographs, many of them showing conditions and scenes no longer existing.

One last point: Here, at long last, is the full record of Nelson and Goldman's travels, accessible to anyone interested, with clues to all the puzzling localities that plagued students of Mexican birds and mammals in earlier years. Goldman's book is a fitting marker to the close of a period in taxonomic work on birds and mammals in this country, when the excitement of exploration and discovery promoted a competitiveness and possessiveness that only interfered with progress. It is one of the tributes to the labors of Nelson and Goldman that today students of Mexican biotas see clearly many of the field problems before them, convinced of the necessity of cooperation and the free exchange of information.

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Intemperate Man in the Tropics [1]

Marston Bates' new book draws a broad picture of the warmer regions of our planet in a somewhat new perspective and offers many valuable and disturbing comments on our current thinking about the tropics. It is written in a cursive and informal though well-disciplined style, free of technical phrasing and soberly but attractively illustrated. Its scope is very wide (it broadens almost beyond relevance to the subject in the last chapter) and the treatment of physical, biological, anthropological, cultural, economic, and political aspects is almost symmetrical. The designs of the book are very aptly drawn in the opening chapter and the issues to be considered are each set in their proper order so that they may be dealt with separately without being out of perspective. Such clearness of purpose is of great advantage to a book that addresses itself to a large public. Each reader is likely to have relative competence in one of the fields over which the study extends and will gain a firmer footing there, whence he can estimate the relevance of the description and interpretation of other fields.

From almost any point of view, however, one will find fault with the delimitation of the tropics as that area encompassed by the 23° 30″ degrees of latitude north and south. The light factor is strictly the only one to be affected in a constantly predictable way by latitude. The other elements of tropicality in places extend beyond and in others fall short of Cancer and Capricorn. One had expected more awareness of this relationship from the author of "The Nature of Natural History." Actually, a brief statement

[1] **Bates, Marston.** 1952. Where winter never comes. A study of man and nature in the tropics. 310 pp. New York, Scribner's, $3.50.

and a diagram are presented on page 97 that make the obvious distinctions, but later the author mentions the pine forests of tropical Honduras (page 177), the tropical civilization of the Incas (pages 71–72) and "gives up" unraveling the tropical from the non-tropical in Asia (page 79). This shortcoming is to be regretted, for the book as a whole offers a personal and objective restatement of tropical problems.

Concerning climate, another major point is not made sufficiently clear: the difference between the warm-moist (typically tropical) regions and other areas to which they are compared resides as much, if not more, in the amplitude of fluctuation as in the lowering of absolute and mean values of temperature and rainfall. Therefore, the "genial" (page 36) climates of tropical areas contrast with the "intemperate" (page 91) climates of the middle latitudes. Equability vs. anomaly as a major item in climatic classification to some extent cuts across the conventional climatological classifications. Thus New Zealand, Northern Coastal California, Western Ireland would not be part of the intemperate zone!

The point, however, which is repeatedly made and stands out as Bates' thesis, is the influence of the cool continental environment and the habits developed by Western man therein on our thinking about the tropics. Our studies, scientific and otherwise, almost all suffer from a strong cultural bias. Very few of us are able to approach flora, soils, ecology, agriculture, economy or politics in the tropical lands by making a direct assessment of the actual elements and factors of the tropical environment itself. Instead, an attempt too often is made to apply directly standards that are workable in the context of our own environment and culture.

With a fine disregard for both authority and orthodoxy (for instance on the subject of race, page 38), Bates uses the acquisitions of the natural and social sciences to develop his thesis and to convey a well-rounded picture of tropical man. This will no doubt displease a number of specialists who would require a more reverent and more thorough utilization of their tenets.

Plant ecologists may regret the unqualified use of the confused term "jungle" which here (page 93) means rainforest, whereas so often it designates dense second-growth and even shrubby grassland. In fact, after the rainforest has been described (Chapter XI), almost nothing is said of other vegetation types in spite of their relevance to man's utilization of the tropical landscape which is the primary objective of the book. On page 243 he writes: "How can the soils be 'poor' that support the most complex vegetative growth known on the planet? It seems to me that it is simply that we haven't learned how to work with the environment." This paradox is far from well understood even by agriculturists and ecologists and would have lent itself to much further development. Our warped ideas concerning soil fertility are much in need of refocusing and the tropical situation offers a perfect test!

Above all, Bates makes out a very strong case for man's mismanagement of his own affairs, for the absurdity of the social customs exalted by Kipling and other colonial educators. A closer scrutiny, of course, reveals that many sartorial and alimentary habits are just as wrong under a colder climate as they are in the tropics. The willingness of man to work strictly within tradition is certainly illustrated no more strikingly anywhere than by the fact that he "has not domesticated any basic food-plant within historic times." Very few geneticists, taxonomists, plant breeders or other biologists have focused their attention and oriented their work in this direction.

Lest some of the reservations made in the paragraphs above underline too heavily what is missing in this book, I shall conclude by saying that the very excellence of presentation, the vividness of style and the interest aroused are the true cause of the conspicuousness of these gaps. From an author who can give us what this book has to offer, we require more! It must be remembered that the book is meant for a general audience. The technically informed will feel that Bates is well aware of most of the controversial points and conflicting interpretations in various fields. But also such a reader may well re-adjust his own sense of proportion and gain a fresh evaluation and new integration of his own ideas.

The following paragraphs contain capital statements (page 239, paragraphs 2 and 3):

"For present purposes, however, we are not so much concerned with the internal problems of western civilization, as with its relation to the tropics. In this, I am always bothered by the Western arrogance, by its assurance that it knows all of the answers and can quite readily fix everything so that the tropical peoples can live happily ever after, if they will only listen. This philosophy underlies all of the various programs of international technical assistance that are so popular these days, and especially the programs of the United States which are aimed at the uplift of practically everybody else."

"I suppose I have been a part of this American missionary movement myself for most of my life, so that it would be ungrateful of me to start throwing stones at it now. But I have taken comfort from the fact that I belonged to the rather small and subsidiary wing of the missionary movement that was trying to learn about things, instead of trying to change things: though I and my fellows have always been

conscious that the things that we learned would, sometime, by someone, be used as a basis for action."

This book is an important contribution for such understanding and a revised plan of action. It is written with a rare independence and an unusual sense of balance. Most scientists are all too readily intimidated by the dicta of "experts" in fields adjoining their own. Because of this they indefinitely delay the achievement of a comprehensive and well-integrated social philosophy. Bates reveals his fully with its main emphasis on Science and its firmest grounding in Biology. The properly political aspect of man's behaviour is visibly more foreign to him and on this he has little to say although he does conduct the reader by quite logical steps out from physiology to ecology, to economics and to politics.

This thread is repeatedly woven through the basic fabric of the book, and the way in which Bates does so shows in him an artistic vein which is not his least asset as a scientist.

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FIELD GUIDE TO THE MAMMALS [1]

Here is what the teacher ordered—a pocket-sized compendium (12 × 19 cm.) on the mammals of North America. The felicitous cooperation of author Burt and artist Grossenheider has provided a most excellent small volume that will be a boon to everyone from the eager Boy Scout to the business or professional man eager for a new avocational interest in his mature years.

After a compact tabular "life list" where each owner may check the species he has seen and a word on "how to use this book," the volume begins with opossums and contains terse characterizations, with measurements and weights, of 373 species in systematic sequence, ending with the beaked whales. The accounts are of species (subspecies being ignored) and the recognition marks for each are followed by brief differentia for "similar species." There are three running continuities—text, distribution maps, and color illustrations, besides sketches of tracks and a few drawings of nests and workings. Each map patterns the current distribution of one or more species without overlap so the reader may quickly visualize the total range. Each plate combines several large or many small species of related forms but individual illustrations are large and clear enough to provide adequate portrayal. The three parts are often closely aligned but in some places the mere mechanics of book making separates text, map, and illustration. Cross referencing, by pages, largely overcomes this inconvenience.

The author has been skillful in compressing text matter to essentials and in the choice of vernacular names. Also, while addressing the non-technical amateur, he has managed to indicate diagnostic features without using the terminology of mammalogists. A plate of line drawings indicating some of these, however, would be useful. Extreme measurements in millimeters also might have been added for the convenience of more advanced students.

Several details that catch the eye of a critical reviewer could be improved in a later edition: The headings for families and for orders shown in the contents and used to subdivide the text should be distinguished typographically; tricolor (p. 6) is scarcely a color; front claws of black bears (p. 32) are short whereas those of grizzlies are long, but both show some curve; sea otters, when present, are on the central California coast (p. 42); the stink (not odor) is characteristic of all skunks (pp. 42–43); a word about recent coyote spread and transplants would be in order (p. 51); the mountain lion still has considerable western forest in which to roam (p. 58) and formerly inhabited the East; also it has alternative vernacular names; the western marmot is the yellow-bellied (pp. 63, 64), and the hoary (p. 64) is a whistler (voices of mammals are rarely mentioned in the book); the Douglas ground squirrel is a distinct species in the "California" complex (pp. 63–69), as separate as many chipmunks; the color differences in valley pocket gophers (pl. at p. 104) and in deer mice (pl. at p. 121) are not "phases" in the sense of black vs. cinnamon bears but differences between species or subspecies; the black (Alexandrine) rat occupies much of the Great Valley of California but doubtfully the desert of southwestern Nevada (p. 137) and the Norway rat is unknown in the latter state (p. 137).

The volume closes with a list of dental formulas, photo-plates of the skull of 101 species, a short list of references to state and provincial publications on mammals, and an index. There is, however, no mention of the now *century old* classic "Quadrupeds of North America" by Audubon and Bachman, the patron saints of American mammalogists.

[1] **Burt, W .H., and R. P. Grossenheider.** 1952. A field guide to the mammals giving field marks of all [North American] species found north of the Mexican Boundary. xxii + 2 + 1–200 pp., illus. (color pls., maps, figs.). Boston; Houghton Mifflin Co. $3.75.

The present book is one in a field guide series under the editorship of Roger Tory Peterson. The latter writes in a prefatory note: "Richard Grosenheider's drawings are so sensitive in handling that one must study them carefully to fully appreciate their artistry." With this sentiment the present reviewer is in complete agreement—but he is unalterably opposed to the terrible blemishes of the "Peterson system" in the form of huge black marks to point at important characters of the various species. These are bad even on a large deer or antelope but they destroy the beauty of portrayal on the smaller mammals. Before the next printing every black plate in the color series should be hand tooled to remove these excrescenses. Also, the printer should seek for closer registry in color printing; the reviewer's copy has unpleasant halos on some of the smaller subjects because of this defect.

Criticisms aside, this is a splendid volume. It will be worn dog-eared in many hands from teachers and Ph.D's down to juniors in college, high school, and the household.

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General Genetics [1]

In spite of the large number of texts on genetics that have appeared in recent years, this book will doubtless find a place and prove to be one of the more teachable texts in the field. It is designed primarily for courses in genetics on the university level, and would be best suited to students who have a fairly good foundation in general biology. The arrangement of subject matter is flexible enough so that an instructor could adapt the text to suit the special interests of his students. In fact, the authors make specific suggestions in the preface as to the chapters that are considered basic to all students and those which could be added for certain groups such as those interested in agriculture, medicine, or fundamental biological research.

The style of writing is somewhat more chatty and intimate than is usually found in college texts. A student may, at times, be frustrated rather than flattered by the numerous paragraphs which open with such a phrase as, "You can easily see, of course,—." One is reminded of the French mathematician, LaPlace, who would frequently dismiss long and complex proofs with the overly optimistic statement, "It is easy to see." However, it is the opinion of this reviewer that the style is very good, and that a student reading the text will have the feeling that the authors are talking to him personally rather than just talking.

The authors state that they have abandoned a historical approach to the subject. This is probably a wise decision, but one cannot help but feel that several very important aspects of the history of genetics have been omitted or treated too casually. For example, the first mention of Mendel's work seems to be on page 30 as an incidental explanatory note among the problems. The only other discussion of Mendel is relegated to about a half page at the end of the third chapter, and nowhere in the book can one find clear-cut statements of "Mendel's Laws." We have made great strides in genetics in this century, but have we progressed so far beyond Mendel that we can let students complete a course in genetics with no notion of what is meant by "Mendel's Laws"? There also appears to be no mention of such important pioneers as Weismann, Bateson, or Sutton. The question of the inheritance of acquired characters is dismissed with a very brief statement, and it seems unfortunate that there is no comment whatsoever on the Soviet controversy over Michurinism versus Mendelism. In the discussion on population genetics, no mention is made of the "Hardy-Weinberg Law" although its principles are stated.

The illustrations by Evan Gillespie are, in general, clear, interesting and artistic. It is regrettable that in a few cases, scientific accuracy is sacrificed for artistic license. Unfortunately, this is the case with the first illustration in the book. It is intriguing to contemplate an obviously male human being, sitting on the beach and looking at a daisy, casually producing a fertilized egg which develops, through several embryonic stages into another human male similarly occupied. Furthermore, it seems misleading to imply that a bean seed, a corn kernel, and a fertilized human egg are analogous, as is done in this figure.

Some of the important genetic phenomena discussed appear to be placed in the wrong chapters to give them proper emphasis. Self-incompatibility alleles, for example, are discussed in the chapter on inbreeding and selection. It would seem that these alleles, found so abundantly among numerous and diverse flowering plants, have sufficient fundamental importance to deserve a more thorough discussion along with other multiple alleles in the chapter on mutations. The cytoplasmic inheritance of male-sterility in onions is a subject that would fall naturally into the chapter on Extranuclear

[1] **Srb, Adrian M., and Ray D. Owen.** 1952. General genetics. x + 561 pp., illus. San Francisco: W. H. Freeman and Co. $5.50.

Inheritance, but is found rather in the chapter on plant breeding. These points are, however, perhaps only matters of taste.

One of the most outstanding features of the book is the treatment of the problems, which the authors rightly consider a "major accessory" to any genetics text. At the end of each chapter, the problems are graded as to difficulty and different groups of problems are clearly set apart with bold face lines. The notes accompanying them are clear and concise. The problems themselves are stated in such a way as to arouse interest on the part of the student, and in some cases even appeal to his sense of humor. This is a rare thing to find in a set of problems!

Of special interest to students of ecology is the fifth chapter entitled, "The Impact of Environment." Chapter 20 on "Heredity in Populations" and Chapter 21, "Genetics and Evolution" should also interest ecologists, particularly since they cover subjects not included in many of the existing texts. Moreover, many references to the interaction between genotype and environment are found throughout the book. A student of ecology would certainly find this text well worth-while for gaining a solid background in the genetic principles so intimately associated with the study of the reactions of organisms to their environment.

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PARENTAL CARE AND ITS EVOLUTION IN BIRDS [1]

This is not the type of bird book one selects for a pleasant evening's reading, but it is chuck full of information that many an ornithologist or behaviorist will thank Dr. Kendeigh for making available, and he will keep it handy on his bookshelf.

Beginning with a short historical sketch of bird behavior studies, the author launches into "the timing aspect of parental care," with which one-half of the book is concerned. Since this is contribution No. 44 from the Baldwin Bird Research Laboratory, one expects to find in it considerable reference to the House Wren. Nor is one disappointed, for in 79 pages, illustrated with 17 graphs and 17 tables, one learns that between 1925 and 1939, 127 separate automatic recordings were made at nests of House Wrens. These involved 1,075 daily, 24 hour records. Incidentally, 428 daily records of 19 other species of birds follow the House Wren's story. Thus the reviewer feels sure the reading public will forgive the author the 13 year digestive period required to assemble the facts into readable analyses, and the published results will either inspire or fatigue the younger ornithologists according to their special interests in the attentive and inattentive periods of birds.

A short chapter of nine pages gives the author's methods for registering automatically the periods which the birds spent on and off their nests in balancing the two great urges of self-preservation (mostly eating) and preservation of the species (care of eggs and young). It is illustrated with one page of clear diagrams, showing the recorders, christened the itograph and the terragraph. The study is obviously a model of its kind, but probably will not soon be duplicated for any other bird. The paucity of similar information for other species is conspicuous when the author reviews the literature for the 19 other species, for which he, himself, has only 428 daily records. The lack of published facts is even more conspicuous in the section of the book entitled, "Evolution of Parental Care." Here he requires only 106 pages to cover the literature dealing with the rest of the 170 families and 8616 species of birds of the world. In this section, however, he has brought together in his customary thorough manner, the published, and even some unpublished, information on the number of eggs laid, incubation periods and parental care, arranged by order and family—a most useful contribution.

In the final section of the book entitled, "Phylogeny and Dynamics of Evolution," the author devotes 24 pages to a summary of the variations that occur in parental care in birds. He comes to the conclusion that while parental care evolved in the animal kingdom to insure a higher survival rate, the development of distinctive and adaptive behavior patterns concerned with the care of offspring came relatively late in the time-scale, after the main taxonomic groups had already become distinct. He goes on to say that for various reasons parental care has reached its highest and most elaborate development in birds.

The volume concludes with 42 pages of references to works cited in the text and 12 pages of index. It is nicely printed on good paper and is remarkably free from errors.

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[1] **Kendeigh, S. C.** 1952. Parental care and its evolution in birds. 356 pp., 35 figs. Urbana: The University of Illinois Press. Illinois Biological Monographs, Vol. 22 nos. 1–3. $4.00 paper, $5.00 cloth.

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ANNOUNCEMENT

8th International Congress of Botany

Paris (France) : 2–14 July 1954

The Congress will be held in Paris from Friday the 2nd to Wednesday the 14th of July 1954. Lodging will be guaranteed according to wishes, in the most comfortable conditions (big hotels) to the most modest (school dormitories).

General excursions and special excursions will take place before and after the Congress. Before the Congress (from 15th to 20th of June) ; North-Africa, Languedoc, Alsace, Lorraine, Nord, Britanny, Normandy, Vendée, Guyenne, Landes, Basque country and Paris area. During the Congress (2nd to 14th of July) : Paris and around Paris (Versailles, Fontainebleau, Chantilly, etc. . .). After the Congress (15th to 22nd of July) : from Paris to Nice via Burgundy, Jura, the Alps, Provence, Massif Central and the Pyrenees. A Post-Congress of 4 or 5 days will take place at Nice (22nd to 25th–26th of July) ; it will be followed by excursions to the Hyères Islands, Corsica, Tropical Africa (Sénégal and Mauritania) and to equatorial Africa (Ivory Coast and Guinea).

The Congress will include, besides the plenary sessions and the sessions on « various subjects », chiefly sessions devoted to limited subjects of actual interest discussed in the form of Symposia.

The stay in Paris and in Nice will include as well many other poles of attraction and interest. Numerous publications, in French and in English, will be presented to the members before, during and after the Congress.

The probable amount of the subscription will be 5.000 francs (or £ 5 or 15 dollars), with a reduced fee for students and persons accompanying members.

All correspondence should be addressed to: Secretariat General Du 8e Congres International de Botanique, 292, Rue Saint-Martin, Paris (3e), France.